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THE UNIVERSITY OF ALBERTA

THE NEARCTIC SPECIES OF NEBRIA LATREILLE (COLEOPTERA: CARABIDAE: NEBRIINI): CLASSIFICATION, PHYLOGENY, ZOOGEOGRAPHY, AND NATURAL HISTORY

by

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A THESIS

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To Beverly, whose love and constant support
have been my most precious resource;
and to Mike, Jeff, Tom, Becky and Katie,
who have shared me with beetles and the mountains.

ABSTRACT

This study, based on examination of over 70,000 specimens, 26 months of field work, laboratory studies, and extensive literature review, brings together available information (through April, 1978) on adult external and genitalic structure, geographical and habitat distributions, phylogenetic relationships, fossil record, and natural history of Nearctic members of the Holarctic genus Nebria Latreille.

Three hundred fifteen structural characters were used to compare representatives of Nearctic species, all nebriine subgenera and 50 other adephagan taxa. Structural characters of the female reproductive system (including genitalia), especially of the bursa copulatrix, spermatheca, and spermathecal duct, were found to be extremely useful for both discrimination and clustering purposes. Characters of male genitalia were also useful for discrimination among taxa, but less so for clustering of same. Intrapopulational dimorphism in hindwing size was not found among Nearctic Nebria taxa; but a complete spectrum of character states of hindwing size and shape (from full-sized/functional to short, scale-like/non-functional) is demonstrated by members of these taxa collectively.

Members of Nebria taxa are cool- or cold-adapted, nocturnal, general predator/scavengers. Taxa occupy more or less restricted life zone ranges (extremes for the genus include Arctic/Alpine and Upper Sonoran Life Zones, but highest diversity is in the Canadian Zone). Members of most taxa live at the margins of swift-flowing streams, but those of some occupy such extreme microhabitats as sea beaches and the margins of alpine glaciers. Members of most taxa characteristically

overwinter as adults, but those of a few taxa do so as larvae. Ambulation is the usual mode of locomotion for these beetles and the importance of flight for fully-winged individuals is yet unclear.

Forty-two native species are recognized for the Nearctic fauna, four of which are described as new: namely, *Nebria gouleti* (type locality--Rattlesnake Creek, Asotin County, Washington); *N. darlingtoni* (type locality--South Fork American River, El Dorado County, California); *N. navajo* (type locality--19 miles sw. of Kayenta, Navajo County, Arizona); and *N. carri* (type locality--Dollarhide Summit, Blaine County, Idaho). A total of 26 additional subspecies are recognized, 22 of which are described as new. A key for identification of adults is included. Only sample descriptions are provided; but a synonymy, bibliography, and complete list of known localities is presented for each species-group taxon.

Among Nearctic species, four main lineages are recognized (namely, the *virescens*, *gyllenhali*, *gregaria*, and *metallica* lineages), and each is also represented in the Palaearctic *Nebria* fauna. These comprise a total of 10 species groups, three of which (the *hudsonica*, *mannerheimii*, and *trifaria* groups) are endemic to the Nearctic Region, seven of which (the *virescens*, *paradisi*, *gyllenhali*, *gregaria*, *obliqua*, *ovipennis*, and *metallica* groups) are shared with the Palaearctic Region. The classification of taxa proposed is tentative, pending reclassification of the Holarctic nebriine fauna. It reflects a "systematization"--system of cladistic relationships suggested by analysis of 171 characters of external adult structure (including genitalia), comprising 670 character states. A "sequencing" convention was used in construction of the classification, to reduce the number of

categories required with no attendant loss of information on cladistic relationship. Determination of polarity and sequence in transformation series of characters was based on (1) "ex-group comparisons", (2) "character correlations", (3) "group trends", (4) "correlation with adaptive significance", and (5) "in-group comparisons" (in order of decreasing importance). These criteria, their application, and all other analytical procedures are discussed in detail. If phylogenetic relationships proposed actually reflect evolutionary history, a total of 1468 extra evolutionary steps (including both convergence and reversal steps) are required to account for the distribution of character states of characters analysed among members of Nearctic Nebria species. Seventy-two percent of characters studied have one or more character states reversed or acquired at least twice independently. Mean number of extra steps per character is 8.702; and some character states have evolved many times (one, for example, at least 36 times). Convergence appears to have been a more frequent evolutionary event than reversal in Nearctic Nebria evolution.

Present known distributions of Nearctic species and species groups are illustrated by dot and line maps, respectively. In North America, members of genus Nebria are restricted to areas north of 30°N latitude. Species and subspecies diversity is highest on the Pacific Coast, especially in Washington, and decreases in all directions from that area, except for secondary centers of diversity in the Sierra Nevada of California and the Rocky Mountains of Colorado and Utah. The fauna of eastern North America is unexpectedly low in diversity. Major centers of endemism include the Cascade Range north of the Columbia River (five endemic taxa), the Sierra Nevada (seven

endemic taxa), the southern Rocky Mountains of Colorado, northern New Mexico and southcentral Wyoming (four endemic taxa), and the southwestern portion of the Colorado Plateau (six endemic taxa). Several secondary centers and subcenters are also recognized and discussed. Distributions of taxa are correlated with mountain systems and not with drainage systems. Similarity in *Nebria* faunas between the Rocky Mountain system and West Coast systems is very low at southern latitudes and increases northward. The northern Rocky Mountain fauna is distinct from but clearly related to those of the central and southern Rocky Mountains, and Sierra Nevada and Cascade Range faunas share a similar relationship. Four groups of geographical range patterns are evident, based on concordance among distributions of species and subspecies. These are: (1) eastern (three patterns); (2) Rocky Mountain (seven patterns), (3) Pacific coastal (nine patterns); and northern and transamerican (four patterns). Vicariance patterns and "individual" and "generalized tracts" evident in the Nearctic Region are described and discussed in detail. Seven individual tracts link sister groups across the northern Pacific Basin and/or Bering Strait.

Striking altitudinal zonation patterns are apparent in montane areas with diverse *Nebria* faunas (e.g. Mountain Rainier, Washington; Yosemite, California; and the Front Range, Colorado). These are described and illustrated.

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My wife, Beverly, has been my unfailing source of strength and renewal. She has patiently endured the frustrations and limitations of graduate student life for so many years, while providing for me and our

children an environment of sustenance and love. My accomplishments are hers as well.

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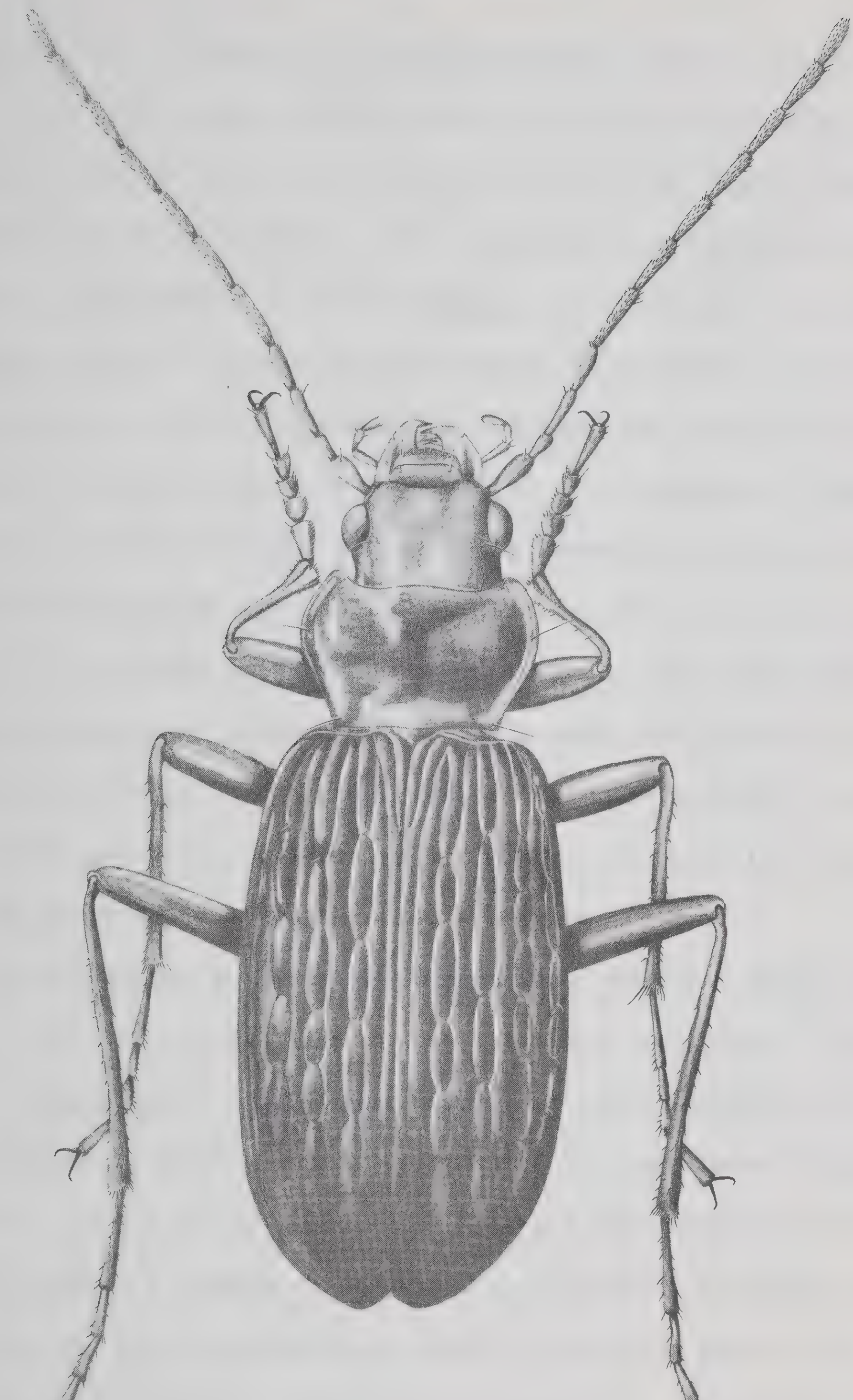
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1.0 INTRODUCTION

My interest in beetles of the genus *Nebria* Latreille began in 1967. While collecting carabid beetles in the Rocky Mountains of Colorado, I concentrated on my own preferred haunts, namely, riparian, nival and peri-nival habitats. This specialization provided frequent encounters with members of various *Nebria* species because, in these habitats, few insect groups approach *Nebria* in abundance. With the aid of Lindroth's (1961) treatment of the genus for Canada and Alaska, I was able to identify most of my material. It soon became evident that *Nebria* species formed a biologically important and interesting element of the montane carabid fauna. Species diversity and population densities in suitable habitats were impressively high; and I began to recognize patterns of altitudinal zonation among the resident species. Observations made on collecting trips in Utah and California suggested that similar patterns of diversity and habitat distribution existed in these and other areas of western North America.

The opportunity to begin serious study of Nearctic *Nebria* appeared in July, 1970, when I enrolled at the University of Alberta. Although Nearctic *Nebria* were, at the time, among the taxonomically better-known carabid groups, I hoped to build on my previous experience through additional studies which seemed both feasible and potentially rewarding scientifically. I planned to obtain data with which to further define the structural and distributional limits of Nearctic species and explore the evolutionary relationships among them. My initial goals were the formulation of an improved infrageneric classification of the New World species and attainment of some basic understanding of the

historical development of diversity and distributional patterns observed in our fauna.

Genus Nebria, in the broadest sense, comprises a group of over 500 nominal taxa which, in aggregate, demonstrate holarctic distribution. The Palaearctic component of the genus is much more diverse, in both species and major lineages, than the Nearctic. Consequently, as discussed below (see sections 3.31 and 5.1), conclusions on the relationships among the New World species and historical development of the fauna would be considered tentative, pending study of the genus in the Old World. Fortunately, as work toward the initial project goals progressed, new sources of taxonomic data became available as by-products of field work and efforts to obtain comparative material on loan. These additional resources permitted expansion of the project to include coverage of the Palaearctic Nebria fauna and the use of additional character systems in coverage of the Nearctic fauna. The latter included external structure of immature stages, life history features (especially life cycle timing) and adult internal structure.

Various facets of the expanded project have progressed at different rates and many studies are yet incomplete or barely begun. This paper represents a first report on the Nearctic fauna. I present here a comprehensive taxonomic treatment of the species, based on characters of adult external and (some) internal structure, distribution and life history features. Phylogenetic and contemporary and historical zoogeographic hypotheses are provided and discussed, and evolutionary trends in the fauna are recognized. Also included are an interim infrageneric classification of the species, reflecting the proposed

phylogeny but pending reclassification of the World fauna, and a preliminary comparative morphology, chorology and natural history of the genus in the New World.

1.1 Historical review of Nearctic *Nebria* systematics

Study of the Nearctic *Nebria* fauna has slowly progressed from a purely descriptive phase (alpha-level systematics) toward a more analytical phase (beta- and gamma-level systematics), a progression characteristic of systematic work in general. However, the second phase has broadly overlapped with rather than simply replaced the first, as illustrated by some early analytical work (see below) and the descriptions of new species-group taxa presented here.

First members of the Nearctic fauna named were those with holarctic distributions, *N. nivalis* (Paykull) (1790) and *N. gyllenhali* (Schönherr) (1806), both described from the Palaearctic Region and originally assigned to genus *Carabus* Linnaeus. Say (1823) was the first North American entomologist to describe an endemic American species, *N. pallipes*. Representatives of many common *Nebria* species were among specimens collected by Eschscholtz [expeditions in 1815 to 1818 and 1823 to 1826] and Vosnesensky [various expeditions during 1839 through 1845] in the Russian New World colonies. Their material was studied, named and described by Dejean (1831), Fischer von Waldheim (1821 and 1828), Mannerheim (1853), Ménétriés (1844) and Motschoulsky (1850, 1859, 1865). Other early descriptions were those of Horn (1870), Kirby (1837), J. Sahlberg (1885) and R. F. Sahlberg (1844). LeConte (1850, 1853, 1859a, 1863a, 1863b, 1866 and 1878) named 11 species, including

the first known from the Sierra Nevada (California) and the Rocky Mountains. Schwarz (1900), Bänninger (1928), Darlington (1930, 1931a, and 1931b), Lindroth (1961), Kavanaugh (1971) and Erwin and Ball (1972) each recognized one or more new and relatively localized species. Casey (1913, 1920 and 1924) provided 26 new names, four (15%) of which I recognize here as valid. Probably the most significant descriptive work on the Nearctic fauna was that by Van Dyke (1924, 1925, 1943, 1949 and 1953). He maintained a life-long interest in the genus, described 12 new species (mainly from material he collected) and amassed the finest *Nebria* collection in North America. His field notes, preserved at the California Academy of Sciences, are both enjoyable to read and a source of supplemental data on his specimens.

Horn (1870) provided the first key to Nearctic species. LeConte (1878) proposed additions to Horn's key and presented new keys to species groups he recognized. Schaupp (1878) repeated Horn's key, incorporating LeConte's additions. Bänninger (1925) included known Nearctic forms in his descriptive keys to subgenera and groups in the World fauna. Hatch (1939a and 1953) provided keys for the northwestern North American species. The most complete and useful key to date has been Lindroth's (1961), nominally for Canada and Alaska but also useful for more southern areas. Erwin and Ball (1972) and Kavanaugh (1971) suggested additions to Lindroth's key.

Efforts at clarification of nomenclatural problems, including designation of lectotypes (or neotypes), were those of Lindroth (1954b, 1961 and 1975 [lectotypes for Casey species]) and Lindroth and Freitag (1969 [neotype for *N. pallipes* Say]).

Discussion of the history of classification of and other studies of relationship among Nearctic Nebria is presented separately, in section 3.3 on classification (see section 3.32).

Zoogeographic analysis of the fauna has been minimal. LeConte (1878 and 1879) and Van Dyke (1919, 1926 and 1940) discussed distributions of Nebria species or species groups and made limited use of these as examples for defining generalized distributional patterns in North American biota. Errors in recognition of relationships among the species, however, reduced the effectiveness of these generalizations. More contemporary and sound zoogeographic treatments of (or including) Nebria are those of Lindroth (1963a and 1963b), Ball (1970) and Erwin and Ball (1972).

LeConte (1878 and 1879) and Van Dyke (1919 and 1926), as usual, were among the first to show interest in the altitudinal distributions of Nebria species. Subsequent studies by Darlington (1943), in the Presidential Range of New Hampshire, Haubold (1951) and Armin (1963), in the Front Range of the Colorado Rocky Mountains, and Spence (1974), in the Green Mountains of Vermont, provided information on the altitudinal ranges of several species.

Comparative studies of Nearctic species have, until recently, dealt only with adult structure. Even isolated descriptions of immatures are few (see Schiødte, 1867 and Larsson and Gigja, 1959). Recent comparative work on larval structure is encouraging. Andersen (1970) described and distinguished the larvae of N. gyllenhali (Schönherr) and N. nivalis (Paykull) in Scandinavia. Luff (1972) provided descriptions of and a key to larvae of the British Nebria

species, including the species named above. Spence (1974) and Spence and Bell (1976) were the first to describe and compare the larvae of American species. Larochelle (1972 and 1976a) and Spence (1974) have presented comparative natural history data on Nearctic species.

2.0 MATERIALS AND METHODS

2.1 Materials

This study is based on the examination of 65,690 Nearctic and 5,818 Palaearctic adult Nebria specimens, 2,374 specimens representing other nebriine genera, and an additional 470 specimens representing an array of more distinctly related or unrelated caraboid taxa (see Appendix C for a list of taxa sampled).

2.11 Materials received on loan

Approximately 35,000 specimens were borrowed for study from various institutional and private collections in North America, Europe and Asia. An effort was made to examine all available material in order to obtain a maximum number of geographical and temporal samples. The following is a list of abbreviations used throughout the text and in Appendices A. and B. which refer to the various collections from which specimens were received. Most, but not all, abbreviations correspond to those proposed by Arnett and Samuelson (1969).

AHab A. Habu, National Institute of Agricultural Sciences, Tokyo, Japan.

ALar A. Larochelle, College Bourget, Rigaud, Quebec J0P 1P0.

AMor A. Morgan, University of Waterloo, Waterloo, Ontario N2L 3G1.

AMNH American Museum of Natural History, New York, New York 10024; L. H. Herman, Jr.

ANSP Academy of Natural Sciences, Philadelphia, Pennsylvania 19103; W. W. Moss.

BFCa B. F. Carr, 5208 32nd Avenue, Calgary, Alberta T3B OJ6.

BMNH British Museum (Natural History), London, England; P. M. Hammond, H. K. Kenward, M. E. Bacchus.

BRot B. Rotger, CR., Immaculate Heart of Mary Church, P. O. Box 451, Pagosa Springs, Colorado 81147.

CArm C. Armin, 191 West Palm Avenue, Reedley, California 93654.

CAS California Academy of Sciences, San Francisco, California 94118; H. B. Leech.

CDA California State Department of Food and Agriculture, Sacramento, California 95814; F. G. Andrews.

CNC Canadian National Collection of Insects, Biosystematics Research Institute, Ottawa, Ontario KlA OC6; R. de Ruette, A. Smetana.

CSU Colorado State University, Fort Collins, Colorado 80521; T. O. Thatcher.

CUB University of Colorado, Boulder, Colorado 80302; H. Rodeck.

CUIC Cornell University, Ithaca, New York 14850; L. L. Pechuman.

DBUM Université de Montreal, Montreal, Québec; M. Coulloudon.

DENH University of New Hampshire, Durham, New Hampshire 03824; W. J. Morse.

DEUN University of Nebraska, Lincoln, Nebraska 68503; B. C. Ratcliffe.

DHKa D. H. Kavanaugh, California Academy of Sciences, San Francisco, California 94118.

DJLa D. J. Larson, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland AlC 5S7.

DRWh D. R. Whitehead, United States National Museum, Washington, D. C. 20560.

DZEC Montana State University, Bozeman, Montana 59715; N. L. Anderson.

EAMa E. A. Martinko, University of Kansas, Lawrence, Kansas 66044.

EDNC North Carolina Department of Agriculture, Raleigh, North Carolina 27602; J. F. Greene.

EMUS Utah State University, Logan, Utah 84332; W. J. Hanson.

ETHZ Eidgenössische Technische Hochschule Entomologisches Institut, Zürich, Switzerland; W. Sauter.

FMNH Field Museum of Natural History, Chicago, Illinois 60605; H. Dybas.

GRNo G. R. Noonan, Milwaukee Public Museum, Milwaukee, Wisconsin 53233.

HGou H. Goulet, Biosystematics Research Institute, Ottawa, Ontario K1A 0C6.

HoKn R. L. Hoffman and L. Knight, Radford College, Radford, Virginia 24141.

HNHM Hungarian Natural History Museum, Budapest, Hungary; S. Horvatovich.

ICCM Carnegie Museum, Pittsburg, Pennsylvania 15213; G. E. Wallace.

INHS Illinois Natural History Survey, Urbana, Illinois 61803; M. W. Sanderson.

ILar I. La Rivers, University of Nevada, Reno, Nevada 89507.

ISUI Iowa State University, Ames, Iowa 50010; R. Miller.

IUIC Indiana University, Bloomington, Indiana 47401; F. N. Young.

JBel J. Belicek, University of Alberta, Edmonton, Alberta T6G 2E3.

JKus J. Kuster, University of Alberta, Edmonton, Alberta T6G 2E3.

JNeg J. Nègre, 9 Boulevard de Lesseps, Versailles, France.

JSch J. Schuh, 4039 Shasta Way, Klamath Falls, Oregon 97601.

JSpe J. Spence, University of British Columbia, Vancouver, British Columbia V6T 1W5.

JVMa J. V. Matthews, Jr., Geological Survey of Canada, Ottawa, Ontario K1A 0E8.

KMFe K. M. Fender, 911 Ashwood Avenue, McMinnville, Oregon 97128.

KSUC Kansas State University, Manhattan, Kansas 66502; H. D. Blocker.

KUSM University of Kansas, Snow Museum, Lawrence, Kansas 66044; G. Byers.

LACM Los Angeles County Museum of Natural History, Los Angeles, California 90007; C. L. Hougue.

LECM Macdonald College, Lyman Entomological Museum, Ste. Anne de Bellevue, Quebec J7V 3N8; V. R. Vickery.

LRus L. Russell, 828 NW 27th Street, Corvallis, Oregon 97330.

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; J. F. Lawrence.

MGF Museum G. Frey, Entomologisches Institut, Tutzing bei München, West Germany; M. Würmli.

MHNG Museum d'Histoire Naturelle, Geneva, Switzerland; C. Besuchet.

MHNP Museum National d'Histoire Naturelle, Paris, France; A. Bons, H. Perrin.

MLLu M. L. Luff, University of Newcastle, Newcastle-upon-Tyne, England.

MSU Michigan State University, East Lansing, Michigan 48823; R. L. Fischer.

NBM Naturhistorisches Museum Basel, Basel, Switzerland; W. Wittmer.

NMDo N. M. Downie, 505 Lingle Terrace, Lafayette, Indiana 47901.

NMPC National Museum in Prague, Prague, Czechoslovakia; Z. Mlynar.

NRSS Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Nyholm.

NSDA Nevada State Department of Agriculture, Reno, Nevada 89504; R. C. Bechtel.

ODA Oregon State Department of Agriculture, Salem, Oregon 97310; R. L. Westcott.

OSEC Oklahoma State University, Stillwater, Oklahoma 74074; W. A. Drew.

OSUC Ohio State University, Columbus, Ohio 43210; C. A. Triplehorn.

OSUO Oregon State University, Corvallis, Oregon 97331; P. Oman.

PADA Pennsylvania State Department of Agriculture, Harrisburg, Pennsylvania 17120; T. J. Henry.

PMCh P. M. Choate, Jr., University of Florida, Gainesville, Florida 32601.

PMNH Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520; C. L. Remington, K. W. Brown.

PSMi P. S. Miliotis, Depot Street Dunstable, Massachusetts 01827.

PSUC Pennsylvania State University, University Park, Pennsylvania 16802; K. C. Kim.

PUCA Pacific Union College, Angwin, California 94508; L. E. Eighme.

PURC Purdue University, Lafayette, Indiana 47907; A. Provonsha.

RCGr R. C. Graves, 627 Crestview, Bowling Green, Ohio 43402.

RCra R. Crawford, University of Washington, Seattle, Washington 98195.

RDav R. Davidson, University of Vermont, Burlington, Vermont 05401.

RFre R. Freitag, Lakehead University, Thunder Bay, Ontario P7B 5E1.

ROM Royal Ontario Museum, Toronto, Ontario M5S 2C6; G. B. Wiggins.

RPPa R. P. Papp, University of California, Berkeley, California 94720.

RTBe R. T. Bell, University of Vermont, Burlington, Vermont 05401.

SFVS California State University, Northridge, California 91324; P. F. Bellinger.

SDSU South Dakota State University, Brookings, South Dakota 57006; E. U. Balsbaugh, Jr.

SJSU San Jose State University, San Jose, California 95114; J. G. Edwards.

TCBa T. C. Barr, Jr., University of Kentucky, Lexington, Kentucky 40506.

TNak T. Nakane, National Science Museum, Tokyo, Japan.

TMZN Tromsø Museum, Tromsø, Norway; J. H. Andersen.

UAFA University of Arkansas, Fayetteville, Arkansas 72701; R. T. Allen.

UASM University of Alberta, Strickland Museum, Edmonton, Alberta T6G 2E3; G. E. Ball.

UBC University of British Columbia, Spencer Museum, Vancouver, British Columbia V6T 1W5; G. G. E. Scudder.

UCB University of California, Berkeley, California 94720; J. A. Chemsak.

UCD University of California, Davis, California 95616; R. O. Schuster.

UCR University of California, Riverside, California 92502; S. Frommer.

UIMI University of Idaho, Moscow, Idaho 83843; W. F. Barr.

UMHF Universitetets Zoologiska Museum Entomologiska Avdelningen, Helsingfors, Finland; H. Silfverberg.

UMMZ University of Michigan, Ann Arbor, Michigan 48104; R. D. Alexander.

UMRM University of Missouri, Columbia, Missouri 65201; W. R. Enns.

UMTF University of Turku, Turku (Abo), Finland; H. Hippa.

USNM United States National Museum, Smithsonian Institution, Washington, D. C. 20560; T. L. Erwin.

UWBM University of Washington, Burke Museum, Seattle, Washington 98105; M. H. Hatch, S. Rohwer.

UWEM University of Wisconsin, Madison, Wisconsin 53706; L. J. Bayer.

UWLW University of Wyoming, Laramie, Wyoming 83070; R. J. Lavigne.

VMKi V. M. Kirk, Northern Grain Insects Research Laboratories, Brookings, South Dakota 57006.

WSU Washington State University, Pullman, Washington 99163; W. J. Turner.

ZILR Zoological Institute, Academy of Science, Leningrad, U. S. S. R.; O. L. Kryzhanovskij, V. G. Shilenkov.

ZMKD Universitetets Zoologiske Museum, København, Denmark; O. Martin.

ZMLS Zoological Institute, University of Lund, Lund, Sweden; C. H. Lindroth.

ZMUM Zoological Museum Moscow University, Moscow, U. S. S. R.; S. Keleinikova.

ZSBS Zoologische Sammlung des Bayerischen Staates, München 19, West Germany; G. Scherer.

2.12 Materials collected for the study

During the period 1969-1975, I collected over 30,000 adult *Nebria* specimens for the study (see section 2.21 for details). Several hundred additional specimens were collected for me by various companions on field trips or by colleagues working elsewhere (see Acknowledgements for a listing of individuals). Their contributions of specimens and field notes added substantially to my own geographical coverage. Of particular importance were collections from the following areas: Queen Charlotte Islands, British Columbia (J. Belicek and M. Pitman); Swan Hills, Alberta (H. Frania and H. Goulet); Appalachian Mountains, eastern United States (R. L. Hoffman); Sierra Nevada, California (D. Giuliani); and Siberia, eastern U. S. S. R. (V. G. Shilenkov).

2.13 Type material

I have been able to study the type specimens of all 85 previously-described Nearctic nominal taxa, through the co-operation of the curators listed above (see Acknowledgements), who provided either work space and access to specimens during my visits to their institutions or loans of specimens. Three minor nomenclatural problems remain unsolved, but none, I think, will require further attention. *Nebria melsheimeri* Sturm (1826:173) and *Nebria eschscholtzii* Sturm (1826:173) (not of Ménétriés) must be considered *nomina nuda* because these names appear only in Sturm's catalog to his collection, unaccompanied by either description or statement of locality; and no type specimens exist. The problem with and current status of the name *Nebria elias* Motschulsky is discussed with treatment of *Nebria gyllenhali*

(Schönherr) (section 3.43 below).

Where necessary, lectotypes have been chosen and so labelled; and their formal designations appear here (see nomenclature sections under appropriate species headings in section 3.43). For a listing of the status and place of deposit of primary type specimens for the Nearctic nominal taxa, consult Appendix A. Holotypes designated for taxa described as new in this study (with the exception of the holotype of N. trifaria utahensis n. ssp.) have been deposited in the collection of the California Academy of Sciences with the Van Dyke Nebria types.

2.14 Fossil Material

A total of 12 fragmentary fossil specimens representing Nebria species were received on loan from A. Morgan and J. V. Matthews, Jr. Together, these specimens constitute the fossil record (to date) for Nebria in the Nearctic Region. In spite of their paucity and relatively low diversity, certain valuable inferences can be drawn from their consideration (see sections 3.24, 3.43 and 4.23 for discussions).

2.2 Methods

2.21 Collection and preservation of specimens

Most of the specimens and natural history data collected for use in this study were obtained on several long expeditions taken each year (1970 to 1974) from May to September. Areas sampled extensively included the Coast Ranges (1971, 1974), the Cascade Range (1971, 1972, 1974), and the Rocky Mountain and Intermountain Regions (1970 to 1973) of western North America. The Sierra Nevada (California) and

Appalachian Mountains, eastern North America in general, and Alaska (interior, Alaskan Peninsula and inner Aleutian Islands) were partially sampled during these expeditions. In July and August, 1972, I spent five weeks in Mount Rainier National Park collecting specimens of and comparative field data on the 14 Nebria species inhabiting the Park. Previous field work in the Rocky Mountains of Colorado (1967 to 1969) provided specimens of and similar comparative field data on the eight species in that area.

For specific information on collecting specimens of particular taxa, consult headings entitled "Habitat distribution" and "Natural History" in the description of each taxon (see section 3.43). In general, individuals are usually found hiding under suitable cover during the day. Typically, they are abundant under small to large stones at the edges of glaciers, snowfields or streams of various size. Because large numbers of specimens can be collected by hand during the day, the use of pitfall traps is unnecessary and usually less effective. Collecting at night with the aid of flashlight or headlamp generally produces fewer specimens but a great deal more natural history data on these nocturnal beetles. Individuals of species which inhabit glacial margins and crevasses or talus slopes can be efficiently collected only at night (when they are active on the surface) because of their inaccessibility to hand collecting during the day.

Adult specimens were generally incapacitated by ethyl acetate fumes, then transferred to and stored in vials containing sawdust or tissue paper and fresh ethyl acetate to await preparation. When adults were sufficiently abundant, specimens were also collected in Weaver's

Fixative (see Ekis and Gupta, 1972) or 70% ethyl alcohol for future studies on internal structures. Other individuals were kept alive for breeding purposes. Results of the breeding program and a study of the immature stages of Nearctic Nebria will be presented in a subsequent paper.

Prior to pinning and labelling, all specimens were relaxed and cleaned in soapy boiling water, then rinsed. Genitalia (median lobe and parameres of males, coxostyli of females) were routinely everted (see section 2.22) at this time but not detached. This procedure permitted the subsequent examination of these structures in thousands of specimens without subsequent relaxation and dissection. When possible, specimens collected in Weaver's Fixative were used for the study of internal genitalic structures (eg. bursa copulatrix, spermatheca).

Older pinned specimens (such as those received on loan) were easily and effectively cleaned of dirt and grease by careful application of a mixture of ammonia, water and a surface tension reducer ("Tergitol") with a fine paint brush. This mixture also relaxed individual body joints and thereby permitted limited rearrangement of appendages as needed.

2.22 Dissecting techniques

Successful examination of the hindwings and genitalia of Nebria specimens usually requires some dissection. Specimens were prepared for dissection by soaking them for five to 10 minutes in boiling water. Addition of a very small amount of detergent (such as "Mr. Clean")

hastened the relaxation process. Specimens collected in ethyl acetate fumes became relaxed easily, but material collected in potassium cyanide fumes or ethyl alcohol sometimes required a brief (two to five minute) treatment in warm potassium hydroxide (10% solution).

A general impression of the size (but not shape) of the hindwings was obtained by simply lifting the left elytron to expose the wing. For a study of venation and wing shape, the left hindwing was torn free at the wing base using fine forceps, then spread and mounted in alcohol on a slide. Permanent mounts (in Euparal medium) were made for all taxa studied; however, most hindwings examined were later dried, glued to cards and pinned with the specimens.

The apex and shaft of the median lobe and the parameres in male specimens or the coxostyli in female specimens were quickly examined in relaxed specimens by simple eversion of these structures using fine forceps. For study of the base of the median lobe in males or the spermatheca, bursa copulatrix and other internal structures in females, the genitalia were extracted as a unit by tearing the membraneous connections between eighth tergum and sternum and the "ring sclerite" (in males) or the valvifers, paraprocts and proctiger (in females). Genitalia were next treated for five to 10 minutes in hot 10% potassium hydroxide solution to remove non-sclerotized tissue, rinsed, further dissected as needed, then transferred to and examined in glycerine. After genitalia were studied and drawn, they were placed in polyethylene microvials in a drop of glycerine and pinned with the specimen.

2.23 Sex determination and association

Determination of the sex of an individual was very simple, requiring only examination of the front tarsi. With some experience, this was done with the unaided eye. Refer to the first couplet (i) in the key to species and subspecies (section 3.422) for characters. No other external structural characters exhibit sex-specific character states throughout Nebria; but sexual dimorphism is present in one or more other characters in some species or species groups (refer to sections 3.41 and 3.43 under "Sexual dimorphism" heading descriptions of taxa).

Males and females of almost all taxa were easily associated by reference to characters of external structure and/or distribution. In those few instances where individuals of two taxa are externally almost indistinguishable and the geographical ranges of the taxa overlap, dissection of the hindwings or genitalia were required to confirm identification and, therefore, association. Fortunately, no two externally similar taxa have perfectly congruous geographical ranges. This permitted the study of internal structures in individuals of each taxon from some locality outside the area of range overlap and subsequent use of observed differences in identifying individuals from the area of sympatry.

2.24 Measurements

The only mensural character used in this study is "standardized body length". This expression appears in descriptions and the key and refers to the sum of three measurements (Fig. 1): length of head,

measured along midline from apical margin of clypeus to a point opposite posterior margin of eye; length of pronotum, measured along midline from apical to basal margin; length of longer elytron measured along midline from apex of scutellum to a point opposite elytral apex. While this measure of relative size avoids error due to variation in extension or retraction of body parts among specimens, it consistently underestimates the apparent total body length of specimens (such as could be measured from the most anterior to the most posterior point) by from 12 to 18 percent.

Range in standardized body length in my sample for each taxon was established by visual selection of smallest and largest specimens for each sex. All measurements were made with a Leitz stereoscopic dissecting microscope at a magnification of 16 diameters, using a calibrated ocular grid with a scale interval of 0.1 mm.

2.25 Illustrations and maps

Line drawings illustrating structural characters were made with the aid of an ocular grid mounted in a Leitz stereoscopic dissecting microscope. Preliminary drawings were penciled on tracing paper placed over a grid of one cm squares. Final inked drawings were then made on heavy weight natural vellum by tracing directly over the preliminary drawings. Unless otherwise noted, scale lines accompanying illustrations equal 1.0 mm. All drawings of homologous structures are consistent in scale and aspect to facilitate comparisons. In some drawings, uniform sparse stippling is used to indicate membranous areas and broken lines represent vague boundaries of sclerotized areas. When

only part of a structure is illustrated (such as the basal region of an elytron), a wavy line serves as the artificial margin.

Scanning electron photomicrographs, used to illustrate various shapes and patterns in microsculpture, were obtained by use of the Cambridge Mark IV "Stereoscan" scanning electron microscope (SEM) in the Department of Entomology, University of Alberta. Specimens were gold-coated prior to examination with the microscope.

Maps are presented to illustrate the distributions of taxa and various geographical (including climatic and physiographic) features, patterns of geographical variation and aspects of zoogeographic reconstruction and analyses. Symbols used on species distribution maps represent approximate locations of samples (refer to Appendix B for listing of sample localities for each taxon).

Wriiten permission was obtained for use of the following maps (or parts of same): Goode Base Map No. 202 (Copyright by the University of Chicago Department of Geography); Landform Map No. 3 (United States) (Copyright by Erwin Raisz).

2.26 Descriptive format

Information about each species is presented in the following sequence: a synonymy (including data on type specimens) and species bibliography; notes on nomenclature and types; derivation of taxon name; diagnostic combination; description of form and structure; sexual dimorphism; geographical distribution; geographical variation; geographical relations with allied taxa; habitat distribution; ecophenotypic variation; taxonomic notes; phylogenetic relationships; dispersal potential; natural history; and fossil record. Presentation

of information on supraspecific taxa (species groups and the genus) follows the same format but with some sections omitted.

The composition, organization and completeness of synonymies and lists of references are discussed below (see section 2.27). Data on the type specimens for all species-group names are ordered as follows: status (as holotype, lectotype or neotype); sex; repository; label data; and type locality. Type localities considered either erroneous or too general (such as a state or provincial record) were emended or restricted respectively. Comments on synonymies, lectotype designations, selection or restriction of type localities and related topics appear under notes on nomenclature and types. Derivations of species-group names are presented only for taxa described as new.

The diagnostic combination is a brief listing of structural and/or distributional character states which, in combination,distinguish members of the taxon from members of other taxa.

Descriptions presented in this study have been arranged so that, by reference to genus, species group or species and subspecies descriptions, the range of character states for any structural character exhibited by members of any taxon can be ascertained by the reader. To this end, the genus description is inclusive, covering the range of character states observed in all characters used for all members of the genus examined. Those characters represented by a single character state or a consistent range of states throughout the genus are omitted from descriptions of lower ranking taxa. Species group descriptions are both inclusive, covering the range of character states for all characters which vary among and within the groups, and

exclusive of characters constant for the genus. Similarly, descriptions of species and subspecies cover the range of character states for all characters (and only those) which vary among members of a species group.

Species and subspecies descriptions presented refer to my concepts of the taxa so ranked rather than to type specimens. The selection and formal designation of holotypes for species-group names is essential to a stable nomenclature. The type serves as the voucher specimen for the name and its application and provides a link between a species name and a certain population or group of populations. Once designated, the type specimen fulfills its role, even if not or only poorly described, because the specimen and the name are permanently associated. Left unassociated, however, are the name and the taxonomist's concept of the taxon of which the type is a member. What requires description, then, is this concept and its limits recognized through the study of variation among taxon members. The extent to which the concepts of taxa reflect their actual properties and limits is dependent on the fidelity of their representation in study samples. Fortunately, my material has been, with few exceptions, quite representative as evidenced by the low incidence of novel variation among new samples received of previously-studied taxa.

For convenience, characters of color and size are treated throughout this study as structural characters although they are really non-structural in the strict sense. Sexual dimorphism, where evident, is treated in a separate section following the description.

The section on geographical distribution provides a brief

statement on the range of the species or subspecies with respect to both political units and boundaries and physiographic features. Maps of distributions and listings of localities for material examined (see Appendix B) provide visualization of and greater detail on distributions respectively. Locality records from the literature which I could not verify with actual specimens are not considered. Consideration of variation associated with geographical distribution presupposes familiarity with distribution and therefore follows treatment of the latter. Sympatry, parapatry and allopatry with respect to related species or subspecies are discussed in the section on geographical relations.

In the section on habitat distribution, the range of microhabitats and altitudinal range occupied by the taxon are discussed and classified according to broad life zone concepts (see also section 3.231). Apparent examples of ecophenotypic variation among members of some taxa are treated in the following section.

Information on the recognition of members of the taxon and/or their separation from members of similar taxa or comments on taxonomic relationship or classification are included under taxonomic notes. Brief comments on proposed phylogenetic relationships are presented under that heading, with more comprehensive treatment deferred to section 4.1 (phylogeny of the Nearctic taxa).

Discussions of the dispersal potential of the taxa are attempts to integrate information on locomotory capabilities with notes on habitat restriction and isolation of populations from other environmentally suitable but unoccupied areas. The section on natural history provides

information on life cycle timing and behavior and notes to aid in collecting members of the taxon.

For those few taxa with a fossil record, data on location and age of deposits yielding specimens are presented together with discussions of past geographical and habitat distributions suggested by the fossil specimens and their respective assemblages.

2.27 Literature and synonymic lists

The results of an extensive review of the literature on Nearctic Nebria appear in the synonymies presented. Each synonymy is a chronological listing of all names which have been applied, correctly or not, wholly or in part, to a species or subspecies here recognized. A history of the status and/or generic placement of these names is not provided. An attempt is made to present a complete bibliography for each species with references listed alphabetically by author after the name which the author used for the taxon. I have probably overlooked some references to Nearctic species, but none have been consciously omitted from the lists. References to both taxonomic and non-taxonomic works (including catalogs, faunal lists, and ecological, physiological, morphological and behavioral studies) have been included.

Although many species-group names have been repeatedly misapplied to various Nearctic taxa, I have been able to re-examine virtually all the specimens involved or otherwise reinterpret literature records. Reference to information provided for each taxon should, therefore, permit accurate interpretation of records of previous works.

2.28 Procedural methods

Specimens obtained by preliminary collecting or on loan were assembled and sorted into clusters based on similarity in characters of size, color and external structure. This rough sorting was facilitated by reference to characters used and clusters recognized by Lindroth (1961). Similarity between males and females of a species-group taxon was generally sufficient to permit inclusion of members of both sexes in the same cluster at this point. Individuals in each cluster were next sorted by locality; and through comparisons of presumptive geographical samples, cluster limits were further defined.

Study of the distributions of samples in all clusters suggested areas in which additional field work might provide taxonomically important data. As time permitted, many of these areas were subsequently visited for the collection of field data and specimens. New material obtained was sorted as described above. Dissections were then made of male and female genitalia and hindwings; and data on habitat distribution for clusters in general and individual geographical samples in particular were examined. Similarities and differences apparent from these studies permitted final adjustments to the limits of clusters. A decision on the status of each cluster and its relationships to other clusters was based on my criteria for recognizing species and subspecies as outlined in section 2.29.

Application of names to clusters ranked as species or subspecies was based on the study of type specimens for species-group names and a review of the literature. Lectotypes were designated and new names provided as required. I examined type specimens for all published

names (see data on types in synonymies, section 3.43).

Species thought to share close phylogenetic relationship, as suggested by analyses using the methods of phylogenetic systematics (cladistics) outlined by Hennig (1966), were grouped in clusters ranked informally as "lineages", species "groups", "subgroups", or "infragroups". Successively more inclusive supraspecific groupings were formed by uniting groups thought to share most recent common ancestry (sister group relationship). This procedure generated a nested hierarchy of strictly monophyletic (Hennig, 1966) [holophyletic (Ashlock, 1974)] groups which served as the basis for the classification presented (section 3.33). Discussions of cladistic theory and analytical methods used and of the relationship between phylogeny and classification are presented in section 3.1 (and 3.31) on classification and in section 4.1 on phylogeny. Additional comments on these and related topics appear in section 3.1.

2.29 Criteria for ranking taxa

Taxonomic categories used in this study and in the tentative classification proposed include the formal ones of subspecies, species and genus and the informal ones of lineage, group, subgroup, and infragroup. Refer to section 3.33 on classification for the rationale behind my choices of particular supraspecific categories.

All available evidence suggests the universality of sexual reproduction among nebriine species. Because apparently all Nebria species are bisexual, I accept as appropriate Mayr's (1969:26) proposed definition of the biological species (as amended by Whitehead, 1972:

139); namely, that species are populations or groups of populations through which gene flow actually or potentially exists, but which are reproductively [intrinsically] isolated from all other such populations [or groups of populations]. As noted by Whitehead (1972:139) and Larson (1975:251-252), the species so defined is a category with a nonarbitrary, objective basis; but this applies only to the extent that interspecific hybridization is excluded or non-introgressive. Success in application of this species definition to the recognition of contemporary species and, therefore, the "objective" bases of taxa recognized depend on the degree to which actual reproductive isolation can be demonstrated or inferred where it exists and excluded where it does not. Direct, unequivocal evidence for this intrinsic isolation or lack of same can seldom, if ever, be provided, even from breeding tests. Only criteria by which indirect evidence can be evaluated are generally useful.

The following working criteria were used in recognizing species. Two sympatric or parapatric forms were considered separate species if all individuals (of one or both sexes) of one differ from all members (of the same or both sexes) of the other in one or more structural characters (other than color or size). In practice, members of sympatric or parapatric Nebria species generally differ in several characters and therefore easily fulfill this criterion. Two allopatric forms were considered separate species if differences between members of each were roughly equivalent to differences between members of two closely related sympatric species, AND if members of geographically intermediate populations of either failed to exhibit intermediate

character states for the differentiating characters. Use of the above criteria requires the following assumption: that continuity or discontinuity in characters of external structure, internal genitalic structure, geographical and habitat distribution, and life history provided by study of population samples (individuals) are evidence of reproductive continuity or isolation, respectively, among natural populations. Clearly, recognition of allopatric species is more arbitrary than distinguishing sympatric or parapatric species; but hypotheses about relationships must be drawn from available evidence, and some estimate about these relationships is preferable to none.

I accept the subspecies definition of Edwards (1959b:230) in slightly altered form: subspecies are populations or groups of populations whose members are recognizably different from members of other conspecific populations and would interbreed with the latter IF they occurred sympatrically and synchronously (under natural conditions) BUT are distinctly isolated from them during their mating periods. The subspecies category was frequently used in ranking allopatric Nebria populations and population groups because patterns of geographical variation are often such that discontinuities in structural and other characters correlate well with discontinuities in habitat or physiography (see also Ball, 1966; and Ball and Negre, 1972). Other workers (Erwin, 1970; Madge, 1967; Noonan, 1973; and Whitehead, 1976) have avoided use of the subspecies category in their studies of lowland, mainland groups. Recognition of the usefulness of a subspecies concept appears to depend on one's particular perspective, more specifically on the distribution of habitats or areas occupied by the organisms one studies. Where gaps between areas of suitable habitat are broad and

clear, such as with predominantly montane groups like Nebria, correlated discontinuity in variation is more confidently recognized and suggestive of active, effective barriers to gene flow.

Because names for subspecies are accorded the same right and strictures as species names and compete with the latter for priority under the present International Code of Zoological Nomenclature, the description of new subspecies (and resultant introduction of new names into the literature) must be justified. I suggest that recognition of subspecies as defined above is justified because they represent incipient species. They are at present independent evolutionary units whose members are differentiated from members of other conspecific populations. Because these units are generally of zoogeographic significance, the formal subspecies trinomen is as welcome a "shorthand notation" (Larson. 1975:252) as the species binomen or other formal names.

In addition to the question of usefulness is one of practicality, recognizing inherent difficulties in the formulation and application of a subspecies concept. The use of the subspecies category has been warmly debated for decades (see for example Brown and Wilson, 1954; Edwards, 1954, 1956a and 1956b; Inger, 1961; and Wilson and Brown, 1953). Without question, great variation in subspecies concepts has existed among taxonomists, such that taxa recognized by various workers are seldom equivalent or comparable units. The inability of taxonomists to formulate and apply a common subspecies concept to their studies is unfortunate but understandable in light of evolutionary theory which predicts a spectrum of intermediate stages in the process of speciation.

Assignment of formal subspecific rank to populations at one particular stage in the process is complicated by the potential for almost infinite variety in evolutionary rate and direction of change.

I agree with Edwards (1954, 1956a and 1956b) that the subspecies as defined above is a relatively objective ("comparatively but not absolutely nonarbitrary" [Simpson, 1961:116]) category. Extensive barriers to gene flow between subspecies can, as suggested earlier, be recognized in some instances through detailed studies of habitat and geographical distribution and life histories. These may in fact be easier to demonstrate than intrinsic isolating mechanisms between distinct species. Arbitrariness arises in decisions on how "different" allopatric or allochronous populations must be for recognition as either distinct species or conspecific subspecies.

Working criteria used for recognizing subspecies were as follows. Two populations or groups of populations were considered separate subspecies if (1) their respective geographical ranges are allopatric and separated by recognizable environmental barriers AND (2) differences between members of each are constant but less distinctive than differences between two closely related sympatric species in one or more characters of structure, color or size AND (3) the geographical pattern of variation in distinguishing characters is non-clinal or distinctly step-clinal. In general, all members of a subspecies can be recognized on structural characters. However, in some instances, where two subspecies were recognized as distinct by a step-clinal pattern of variation, all members of one subspecies may be distinguished only from all members of the most proximate populations of the other (see for

example the subspecies of Nebria lacustris Casey). The following assumption is required with use of the above criteria: that the amount of phenotypic divergence between two allopatric populations is a measure not only of the completeness and duration of their extrinsic isolation but also of the probability that reproductive (intrinsic) isolation has evolved between them. Where this assumption is invalid, the resultant error in ranking (i.e. recognizing as subspecies taxa which in fact conform to the biological species definition) is less objectionable than its opposite. If ranked as subspecies, close relationship between the taxa is emphasized,and species-group names are provided and protected by priority, requiring only change in status should actual relationships be determined later.

The informal categories of infragroup, subgroup, group, and lineage were used respectively in ranking successively more inclusive monophyletic groups. Monophyly and sister group relationships were suggested by phylogenetic analyses (see section 4.1 on phylogeny); and the method I used for representing these relationships in the formal classification is discussed in sections 3.31 and 3.33 below. Formal ranking required subjective assessment of the distinctiveness and breadth (internal divergence) of supraspecific taxa (without regard to taxon size) in the absence of more objective data on the timing of the proposed branching sequence (cladogram, section 4.13). Hennig's (1966) minimum age criterion for formal ranking is non-arbitrary, but at present generally inapplicable, especially for infrageneric classification.

3.0 SYSTEMATICS

3.1 Introduction

Systematics, as defined by Simpson (1961), is "the scientific study of the kinds and diversity of organisms and of any and all relationships among them". So defined, systematics is a master discipline which embraces taxonomy and all comparative aspects of biology. Included in this section is a diverse group of topics, all of which are clearly within the province of systematics.

The results of various comparative studies (morphology, chorology, etc.) presented represent preliminary attempts toward a broad comparative biology of *Nebria*. Data generated by these studies have also served as the bases for the key, descriptions, classification and analyses presented here.

Simpson (1961) defines taxonomy as "the theoretical study of classification, including its bases, principles, procedures, and rules". This definition, with which I agree in principle, depicts taxonomy as a purely theoretical discipline, while Mayr's (1969) definition (that, "taxonomy is the theory and practice of classifying organisms") comes closer to the more widely held concept of the term. In practice, taxonomy embraces not only classification ("the ordering of [organisms] into groups (or sets)...." (Simpson, 1961)), but also naming of taxa (i.e. nomenclature) and description and identification (including construction of keys) of individuals.

A preliminary classification of Nearctic *Nebria* is presented in this section, followed by a key for the identification of members of included taxa and a nomenclatural, bibliographic and descriptive

treatment of same. As discussed below (see sections 3.31 and 4.11), the classification is based on the results of cladistic and zoogeographic analyses (section 4.0). The analyses, although prerequisite to the classification and properly included under systematics, are presented separately (with discussion of evolutionary trends in the fauna) for ease of access, in anticipation of interest in these topics among biologists with little or no interest in _Nebria_ classification _per se_.

3.2 Comparative Biology: Character Systems

Because the essence of systematics is in comparison, its data must be strictly comparable. Hennig (1966) introduced the term _semaphoront_, defined as "an individual at some specific, given point in the developmental sequence" (Kavanaugh,1972), to emphasize the importance of restricting comparisons not only to equivalent (homologous) traits of different organisms but also to equivalent developmental stages among them.

The bases of comparison used by systematists are traditionally called _characters_; and the particular manifestation of a given character in any individual is one _character state_ of that character. The recognition and use of particular characters depends on the kinds of comparative studies made (e.g. morphology, embryology, etc.). Each different study results in the generation of a different set of characters, a _character system_. Use of combinations of character systems in taxonomic and evolutionary studies has increased in recent years (see for example the works of Brothers (1975) on mutillid wasps

and Goulet (1974) on the species of subgenus Bothriopterus (Carabidae, genus Pterostichus)), a most welcome and potentially fruitful trend away from classical "single character" or 'single system' taxonomy.

In this section, I present results of the following comparative studies on Nearctic Nebria: morphology (study of form and structure); chorology (study of geographical distribution); natural history (study of life style); and paleontology (study of fossils and their temporal and spatial distribution). These studies permitted either widespread or limited (as noted) use of characters from the following character systems: adult external form and structure; adult internal form and structure (limited); contemporary geographical distribution; historical geographical distribution (limited); contemporary habitat distribution; historical habitat distribution (limited); life history; mating behavior (limited); feeding behavior (limited); and locomotion (including dispersal capabilities) (limited). I have tried to make appropriate use of the diverse data available from these studies in the analyses and construction of the classification by first recognizing their respective limits. Data on form, structure and date and locality of capture of adults were available for almost all specimens examined. Natural history data were available for approximately half of the material studied (i.e. that material collected specifically for the project) and were, therefore, representative of fewer and/or smaller samples. Fossil specimens (see section 3.24) are limited in both quantity and their temporal and spatial representation; and, consequently, data resulting from their study were generally of limited use.

3.21 Comparative morphology

It follows from the discussion in section 3.1 that, for systematists, comparative morphology is the study of characters of form and structure. A total of 315 adult structural (including color and size) characters were recognized and used in this study. Sixty-six of these are represented by a single character state among Nearctic *Nebria* species. My coverage of external structure was broad and, generally, in detail; but study of mandibular and maxillary structure was superficial. Careful comparative study of these mouthparts will undoubtedly yield additional useful characters, especially if an effort is made to relate structural with functional differences [For example, Evans (1965a, 1965b, 1965c) has related mouthpart structure to feeding behavior in *N. brevicollis* (Fabricius) adults].

Study of internal structure was limited to the genitalia and associated structures: median lobe and parameres of males; ovipositor, bursa copulatrix, common oviduct, spermatheca and spermathecal duct of females. Shape of the internal sac of the male median lobe was not routinely examined, although potentially useful characters were recognized in this structure. Meaningful interpretation of inter- and intraspecific variation in both internal sac shape and shape of the bursa copulatrix in females must wait *in copulo* studies to ascertain correspondence of parts. Previous studies of internal structure in *Nebria* have been limited to the digestive system (Carleton, 1936; and Erwin and Ball, 1972), pygidial defense glands (Forsyth, 1972), parts of the female reproductive system (Erwin and Ball, 1972), and the neuro-endocrine complex (Ganagarajah, 1965), all (except the work of

Erwin and Ball) on members of _N. brevicollis_ (Fabricius).

3.211 General characters

Size

Among the Carabidae, members of _Nebria_ species are medium-small to medium-large in size. Within the genus, size range is considerable and frequently a useful taxonomic and/or key character. Range in size (standardized body length) of Nearctic species is from 6.7 to 14.9 mm; but species with small or larger members are found in the Palaearctic fauna.

With few exceptions, body size class (i.e. small, medium or large size) is relatively constant within species groups and subgroups. For example, most Nearctic species whose members are large belong to the same species group. Females are usually larger than males of the same species; but the reverse is true for members of both subspecies of _N. ingens_ Horn. Intraspecific size variation is considerable in some species, but intrapopulational variation is great in only a few species. Examples of geographical and suspected ecophenotypic variation in size are discussed under descriptions of taxa involved and in section 4.4 on Evolutionary Trends.

In general, proportions of adult individuals remain constant regardless of body size. In some species (see for example descriptions of _N. lacustris_ Casey and _N. nivalis gaspesiana_ n. ssp.), pronotal shape appears to change with increased size; but other examples of apparent allometry were not found.

General form

These beetles are generally slender in form and delicately structured, most markedly resembling the Agonini in habitus. Variation in general form among Nearctic species is slight compared to that in the *Nebria* fauna world-wide. The head and pronotum are generally short in relation to elytra, but the relative sizes (lengths or widths) of these parts are extremely useful characters (see also below). Sex-associated variation in relative head size or relative elytral length is apparent in several species. With few exceptions, appendages are slender and elongate.

Of the four general types of body form recognized by Jeannel (1926; see also Erwin, 1970), two are found among members of the Nearctic *Nebria* fauna. These are:

1. *Type ailé* (long-winged type) (Fig. 2)-- eyes large, pronotum short, elytra rectangular with base broad and humeri prominent, metasternum long.
2. *Type aptère* (short-winged type) (Fig. 3)-- eyes large or small, pronotum long, elytra ovoid with base narrow and humeri flattened, metasternum short.

A complete spectrum of intermediates between these two types of body form is also found among members of the fauna. Pigmentation does not appear to be correlated with body form in Nearctic *Nebria* as it does in some other groups (see Erwin, 1970; Jeannel, 1926). For additional discussion on the suite of characters associated with evolution of brachyptery in *Nebria*, see section 4.4.

Color

Color (pigmentation) characters are extremely useful in working with Nearctic Nebria. Range in body color is from pale yellow to black. Head, pronotum, elytra, venter and appendages are most often concolorous, although shading varies among parts in some taxa (for example, more proximal articles of all appendages usually grade to a darker shade of the same color than more distal ones). However, marked contrast in colors of different parts is evident in members of some species. Most commonly, the elytra and other appendages (most noticeably the legs and antennae) are involved in these contrasting patterns. A number of species have all members with contrasting pale appendages, while others are dimorphic for appendage color (i.e. members of the same population have all appendages either pale or dark). Still others are polymorphic for this character (members are either concolorous, or the pattern is strongly contrasting, or some intermediate condition is exhibited); and this variation is either random (intrapopulational) or geographically correlated. Members of fewer species exhibit the contrasting pale elytra pattern. Species dimorphic or polymorphic for this character are known, but no Nearctic species has all members with contrasting pale elytra. The pattern is usually correlated with geography and habitat (see also section 4.4 on Evolutionary Trends).

An important taxonomic character is the presence or absence of "red spots" on the frons. These spots are actually faintly- or non-pigmented areas and their presence can only be recognized in species whose members have dark head color. The spots, if present, are small,

paired and paramedial (Fig. 4) in most members of most species; but they are broadly fused as a single, larger median spot (Fig. 5) or incompletely fused (anteriorly only) forming a vaguely M-shaped spot (Fig. 6) in a few members of some species and all members of a few taxa.

For up to seven weeks following eclosion, adults are teneral (i.e. soft and not fully pigmented). This provides a source of error in evaluating color in individuals. In general, hardening of the cuticle and deposition of pigment are roughly synchronous, and most suspected teneral adults are distinguished from pale matures by their softness and pliability.

Reflection

I use the term 'reflection' for the apparent metallic coloration seen in members of many Nearctic species. This visual effect (metallic color) is produced as light passes into and is reflected by various layers of the cuticle (Gilmour, 1970). The particular spatial relations among cuticular layers and the nature and content of intervening spaces account for absence of the effect or its presence, intensity and hue. I reserve the simple term 'color' (as discussed above) for pigmentation. Color and reflection are quite independent characters, the only apparent correlation between them being that metallic reflection is always associated with dark color (rufous to black).

When present, reflection is metallic blue, or violet, or red, or green, or suggested as brassy or copper highlights. It is most commonly seen and intense on the elytra, less common and intense on the pronotum and head, rarely present on the venter, and absent from the appendages.

Reflection is frequently very faint and difficult to recognize. Differences in lighting and condition of specimens may alter its perception. For consistent results, clean, dry specimens should be viewed under natural or fluorescent light. Maturity of the specimens can also affect reflection. Some teneral adults exhibit faint metallic reflection even if mature adults of the same species are brilliantly metallic or totally non-metallic.

Luster and microsculpture

The luster (shininess, dullness or iridescence) of dorsal body surfaces is useful on its own for distinguishing members of some species, although it is merely a visual effect dependent on the so-called microsculpture of that surface. Range in luster among Nearctic Nebria is from very dull to faintly iridescent. In general, individuals exhibit a slight increase in dullness (or decrease in shininess) from head to pronotum to elytra. In comparisons among individuals and taxa, therefore, luster of the same respective body regions must be examined. Iridescence is quite rare and faint in Nebria and, when present, restricted to the elytra or abdominal venter.

Microsculpture (Figs. 7 - 12) refers to the surface pattern of microlines and areas delimited by them. The patterns of lines are called meshes, probably because they resemble wire mesh patterns. The meshes vary in continuity (whether broken or unbroken), depth of impression (from absent to deeply impressed) and shape (from 'isodiametric' (Fig. 7) to slightly to markedly transverse (Figs. 9 - 11) to present only as transverse lines and interspaces with little or no mesh-like appearance (Fig. 12)). In fact, areas

delimited by meshes, the alveolae, rather than the meshes themselves, actually have shape; but the tradition of referring to mesh shape is followed here for conformity with other recent studies. Convexity of alveolae, however, is described, ranging within the genus from flat (Fig. 8) to slightly convex (Fig. 7).

A transition is generally evident within individuals in microsculpture (just as in luster) from head to pronotum to elytra. In general, depth of impression of the meshes increases from head to elytra. In addition, meshes, if present, are isodiametric on the head, and of most individuals on the pronotum, independent of mesh shape on the elytra. Comparisons of mesh shape are, therefore, meaningful only for the elytra. For consistency, observations of microsculptural characters were made in the following areas: frons, vertex, clypeus and labrum (at longitudinal center of each, just left of midline); pronotum (at longitudinal center of disc, midway between midline and left lateral margin); and elytra (at a point one-fourth the elytral length distant from the basal margin and centered on the third, fourth, or fifth interval.

Pubescence

Members of Nearctic Nebria are without pubescence except on the fifth through eleventh (flagellar) antennomeres (also on apex of fourth antennomere in a few individuals of N. virescens) and on the ventral surfaces of the basal two or three tarsomeres of anterior tarsi in males. Setae, relatively abundant and taxonomically important, are discussed with the parts which bear them.

3.212 Head

Frons and vertex

Frontal characters, useful in studying many other carabid groups, are of little importance among _Nebria_. Within the genus, convexity varies slightly (frons is moderately convex in members of most species, almost flat in those of a few) and macrosculpture (frons is completely smooth in most members of all species but faintly rugulose laterally in some individuals). A single pair of supraorbital setae is present in members of all species, one positioned medial to the posterior margin of each eye (Fig. 13). The frontal furrows are evident (Fig. 13), although shallow, broad and vague in many individuals. In all members of some species (e.g. _N. ingens_) and some members of many other species, the furrows are present only as short, moderately deep foveae (Fig. 22).

The vertex in members of all species is smooth and moderately convex. In at least some individuals in all species, a faint median foveate or transverse impression is seen.

Genae

Among carabids, relative enlargement (swelling and broadening) of the genae is often associated with decrease in eye size in many species. This inverse relationship maintains among Nearctic _Nebria_ also. In all species, the head width across the genae is greater than across the frons anterior to the eyes (Fig. 18). With even moderate reduction in eye size (see below), broadening of the head behind the eyes is evident, reaching an extreme in males of _N. ingens_ (Fig. 22) where the post-orbital maximum head width is

greater than the width across the eyes.

Sex-associated variation in head width across the genae is present in several species. In these taxa, females are relatively broader than males, except in N. ingens (where the opposite pertains).

Occiput

Among Nearctic Nebria, the occipital region is not constricted to form a "neck" as in members of some Leistus species and a few Palaearctic Nebria species. In general, variation in width across the occiput mirrors variation in head width across the genae; and sex-associated variation is the same as with the latter (see above).

Eyes

No nebriine species is known to have eyeless members, although those of Nebria nudicollis Peyerimhoff (from the Djurdjura Mountains, Algeria) have very small (yet still multifaceted) eyes. Members of most Nearctic Nebria species have medium-sized (in diameter) eyes (Fig. 18), but those of a few species have eyes slightly to moderately reduced in size (Fig. 19). In members of all Nearctic species, eyes are convex, protuberant; but interspecific variation in this character is evident. The most markedly convex eyes are seen in members of N. appalachia Darlington (Fig. 17) and the least convex members of N. ingens (Fig. 22).

Antennae

In general, the antennae of members of Nearctic Nebria are elongate and filiform. Interspecific variation is evident, however, in relative antennal length and in the shape, number of setae and (in one instance) pubescence of various antennomeres.

In assessing relative antennal length, a standard comparative measure was needed. I chose to relate antennal length to body size in a manner illustrated in Fig. 23. If the antennae are relaxed, bent at right angles distal to the scape and stretched posteriorly along the dorsum, their length is estimated by reference to the points of insertion for the middle and hind coxae. Length classes and grades of each were recognized. In members of most Nearctic species, antennae are medium-length or long, slightly shortened or very long in members of only a few species. Males of all species have relatively longer antennae than conspecific females, although the difference is slight in most species.

Shape of the antennal scape is an extremely useful character (Figs. 24 - 41). Members of some closely related species or different subspecies differ greatly in scape shape. Three aspects of shape are important: relative length, symmetry (whether straight [Fig. 32], arcuate [Fig. 41] or bisinuate [Fig. 25]), and diameter (whether cylindrical [Fig. 34], oval [Fig. 24], apically [Fig. 30] or basally [Fig. 28] narrowed or anteriorly swollen [Fig. 27]). Among members of Nearctic species, antennomeres are approximately round in cross-section (except in members of _N. ingens_, in which the second through fourth antennomeres are laterally compressed basally [Fig. 43]). Flagellar antennomeres (i.e. fifth to eleventh) vary slightly but consistently in shape (relative length) even among members of some closely related species or different subspecies.

Pubescence is restricted to the fifth through eleventh antennomeres in all members of Nearctic species, except for a few individuals of

N. virescens which have scattered pubescence also on the apex of the fourth antennomere (Fig. 44). The scape bears a single subapical, anterodorsal seta (Fig. 24) in members of all species, and the pedicel a single ventroapical seta (Fig. 45) in those of all but a few species. In the latter, members have instead two to four apical setae (Figs. 46 - 47).

Clypeus

The clypeus is similarly-shaped in members of all Nearctic species, with the anterior margin approximately truncate (Fig. 48) or weakly concave (Fig. 49). In all specimens examined, a single pair of paralateral setae was present, and the fronto-clypeal suture was clearly evident and complete (Fig. 48).

Labrum

The labrum is rectangular, with three pairs of setae across its anterior margin (Fig. 50) in members of all species. The medial pair is short and fine, the lateral pair longest, and the middle pair more varied in length and thickness. Variation in shape of the anterior margin is considerable within and between taxa, but of little systematic importance. The margin is approximately truncate (Fig. 50) or weakly convex (Fig. 51), concave (Fig. 52) or bisinuate (Fig. 53), with all possible combinations found among members of one species or another.

Mandibles

All Nearctic Nebria have mandibles which are basally trigonal, apically subfalciform and slightly asymmetrical (Figs. 54 - 59). Each mandible bears a large, sharply defined unisetose scrobe. The

apex of the terebral blade of the left mandible is moderately (Fig. 54) to markedly (Fig. 55) angulate medially (i.e. hooked), while that of the right mandible (Fig. 57) is evenly arcuate (not hooked). In members of most species, the basilateral area is narrowly explanate (Fig. 57); but in members of a few species (e.g. N. hudsonica LeConte, N. pallipes, this area is moderately broad (Fig. 59) and vaguely reminiscent of such development in members of Leistus species.

As noted above, detailed comparative study of the medial (cutting) margins and associated structures of the mandibles has not been made. A general survey of structure in Nearctic Nebria compared with members of related genera and tribes permits, however, the following synopsis. [Terms are those of Ball, 1959.] The terebral margin of each mandible is long and weakly concave, terminating basally in a moderately (Fig. 57) to strongly (Fig. 58) developed tooth. In general, this and all other teeth are more strongly developed on the right mandible than on the left (Figs. 54 - 59). The retinacular ridge is short, not or only slightly extended distal to the retinacular tooth and ventral to the terebral margin. The retinacular tooth is present as a vague, broad marginal swelling (Fig. 54) or well defined and dentiform (Fig. 56); and on the right mandible, it is very long and projected (Fig. 58) or moderate in length. In the molar region, a premolar tooth is evident (Fig. 56) or not (Fig. 54) on the left mandible; but this tooth is not developed on the right mandible. At the base of the molar region, a markedly developed tooth (of unknown homology) is present on each mandible (Figs. 57 - 58). A setiferous ventral groove

is present on each mandible, extended longitudinally, parallel to the cutting edge and teeth and separated from these by a trough which is sharply delimited laterally and medially continuous with the horizontal plane of the edge (Figs. 57 - 58). The medial (oral) basal margin of each mandible is excavate; and the connecting membranes bear patches of fine setae (Figs. 57 - 58). Erwin (1970) illustrated mandibles (see his figure "5.") with setae in a similar area in certain Brachinida; but his representation suggests that, in those beetles, the setae are on the mandible itself rather than on a connecting membrane.

Maxillae

Among Nearctic species, the maxilla (Fig. 60) exhibits little variation. Although detailed interspecific comparisons have not been made, a general survey of selected taxa indicates that slight differences in number and/or arrangement of spines and setae on the cardo, stipes, lacinia, palpiger and palpus may characterize some species or species groups. Differences in relative lengths of different maxillary palpomeres may also prove useful.

The setiferous spiniform ventral processes characteristic of members of Leistus species are entirely lacking from all Nebria.

Labium

Structural characters in the labium are extremely useful in distinguishing and grouping nebriine and related genera; but interspecific differences are usually slight and often inconsistent. Several characters are, however, useful in defining species groups and in distinguishing members of certain species.

The ligula (Figs. 61 - 63) is roughly quadrate or faintly

trapezoidal in outline, longitudinally keeled ventrally, the keel terminated apically in an anteroventrally projected tooth in members of most species. Two apico-medial setae are found in members of all species, usually associated with the tooth. The anterior margin is truncate (Fig. 63) or anteriorly projected medially in association with development of the keel tooth (Fig. 62) The paraglossae are indistinct, completely fused with the ligula (fused glossae) (Fig. 62) except in _N. virescens_, members of which have minute but distinct dentiform lobes at the apicolateral angles of the ligula (Fig. 61).

The palpi (Fig. 61), comprised of three filiform palpomeres, articulate basally with the palpigers, the latter connected by membranes to the base of the ligula and the anterodorsal margin of the mentum. The penultimate labial palpomere is equal to or slightly less than the terminal palpomere in length and, in members of most species, bears three setae on its anterior surface (Fig. 62). Members of a few species have only two anterior setae (Fig. 61).

The shape of the mentum (Figs. 64 - 78) is similar in all species. The anterior margin is deeply emarginate and toothed medially. Depth of the emargination varies within and between species, occupying from one-third (Fig. 65) to one half (Fig. 71) the total length of the mentum. The medial tooth is bifid in members of most species, although tooth length and depth of the apical notch vary within or between certain taxa. It is roundly truncate, however, in members of _N. ingens_ (Fig. 76) and only slightly emarginate apically in members of _N. ovipennis_ LeConte (Fig. 75) and related species. The epilobes are broad, smoothly rounded laterally and anteriorly, each terminated

apicomedially in a sharp tooth. Interspecific variation in development of the tooth is considerable, ranging from a minute projection (Fig. 70) to a long, stout spike (Fig. 74). A maximum of four pairs of setae, each with characteristic position are seen on the mentum in members of nebriine genera. All four pairs are in members of genus Leistus, but no more than three among those of Nebria species. Chaetotaxy of the mentum is illustrated in Fig. 64. Members of all Nearctic Nebria lack the M4 setae (Figs. 65 - 78). The occurrence and position of M1 and M3 setae are constant in all members (except those of N. carri n. sp. in which the M3 setae are absent [Fig. 72]). M2 setae are present in all members of all taxa, but variation in their position is a useful character. In members of most species, M2 setae are positioned about two-thirds the distance from the base of the mental tooth to the base of the mentum (Fig. 77). Variant positions are: (1) more apically, at about half the distance from the tooth base to the base of the mentum; or (2) basally, adjacent to the basal margin (Fig. 65).

The gula (Fig. 79) is T-shaped, smooth, without the setiferous spiniform processes or ridges characteristic of members of genus Leistus. A row of setae traverses the broad anterior region. Inter- and intraspecific variation observed in both number and position of these setae was so great as to preclude formulation of a chaetotaxic scheme as was done for the mentum. A rough distinction is made, however, between 'medial' and 'lateral' pairs of setae (Fig. 79). Among members of Nearctic species, number of medial pairs ranges from zero to two and of lateral pairs from one to seven. Number and position

of these setae are quite constant among members of a few species; and in N. ingens, sex-associated differences in the numbers of both lateral and medial setae were apparent. In general, however, characters based on gular setae are unreliable.

3.213 Prothorax

Pronotum

Shape of the pronotum (Figs. 82 - 122) is an extremely useful character. Seemingly strong differences in habitus among individuals of a single species or those of different species are often found to involve only slight differences in pronotal shape. In members of N. virescens, the pronotum (Fig. 84) is semiovoid, not noticeably narrowed basilaterally. In members of all other Nearctic species, the pronotum is basically cordate, with interspecific variation in shape (ranging from faintly[Fig. 120] to very markedly [Fig. 111] cordate) common. Terms used in reference to the pronotum are illustrated in Figs. 82 - 83 . The pronotal disc is convex (but in members of some species more weakly or strongly so) and smooth, except in a few species in which some individuals have the disc very faintly punctulate (e.g. N. vandykei Bänninger).

Intraspecific variation in shape of the apical (anterior) margin is considerable, ranging among members of some species from truncate to convex or weakly concave medially. Interspecific variation in the anterior margin is too inconsistent to permit use of this character in comparisons among most species.

The lateral pronotal margin is arcuate, varying among members of different species from faintly to markedly so. In members of

N. lyelli Van Dyke (Fig. 94) and unique to them, is a shallow subapical sinuation in the margin. In all members of most species the margin is sinuate sub-basally, with considerable interspecific (and moderate intraspecific) variation evident in the depth and length of the sinuation (Figs. 84, 87). It is entirely lacking from or very shallow (Fig. 101) in members of a few species (e.g. *N. virescens* or *N. obliqua* LeConte). Width of the lateral explanation of the pronotum (delimited medially by the lateral groove) is also a useful character. Intraspecific variation is slight and interspecific variation considerable. The explanation may be of equal width throughout (Fig. 116), ranging from narrow to broad, or either narrowed or broadened anteriorly and/or posteriorly. Almost all combinations of the above are seen among members of one or more species (Figs. 84 - 122).

Shape of the basal (posterior) margin is related in part to shape of the basal (lateral) angles (see below). In members of some species, the margin is truncate (Fig. 84) or weakly bisinuate and concave medially (Fig. 111). In other species, members have the margin weakly concave (Fig. 94) or convex (Fig. 85), bisinuate and weakly convex medially (Fig. 87) or weakly (Fig. 105) to strongly (Fig. 100) sinuate laterally. Relative length of the margin is dependent on the degree to which the pronotum is constricted basally (see above).

The apical pronotal angles vary among Nearctic species in length (degree of projection anteriorly), width and shape of their apices. These three characters vary considerably interspecifically; but they have been most useful in distinguishing closely related species or

different subspecies. Intrapopulational variation is generally slight. In members of different species, range in length of the angles is from short (Fig. 103) to long (markedly projected) (Fig. 111); in width, from narrow (Fig. 94) to broad (Fig. 103); and in shape of the apices, from broadly rounded (Fig. 84) to bluntly pointed (Fig. 94).

Shape of the basal pronotal angles is also an extremely useful character. In members of most species, the angle is rectangular (Fig. 97), in those of a few species acute (Fig. 115) or obtuse (Fig. 101). In addition to degree of angle, the basal angles vary in degree of posterior projection, from not (Fig. 122) to markedly (Fig. 111) projected. The apices of the angles are themselves simple (Fig. 122) or denticulate laterally (as in _N. paradisi_ Darlington, Fig. 86) or posteriorly (Fig. 115).

Anterior margination (Fig. 82) of the pronotum is present in members of all Nearctic species (absent only from a few members of _N. zioni oasis_ n. ssp.), but not defined on the medial one-third of the apical margin. Width of the margination is relatively constant (Fig. 116), narrowed (Fig. 97) only in members of some species in the _sahlbergii_ group. Definition of the margination is also relatively constant, but more or less marked in members of a few species. Lateral margination (the "lateral bead" of Lindroth, 1961) is complete, uninterrupted (Fig. 94) in most members of most species, basally obliterated (Fig. 103) in some members of some species and all those of others (e.g. _N. virescens_). Margination width varies within and among species from uniform throughout (Fig. 94) to apically (Fig. 95) and/or basally broadened. Variation in definition of the

lateral margination is similar to that for the apical margination. Posterior margination is absent from members of all species studied.

Inter- and intraspecific variation in depth (from shallow to deep), definition (from broad and vaguely defined [Fig. 84] to narrow and sharply delineated [Fig. 103]) and macrosculpture (from smooth to moderately punctate) of the anterior transverse impression is considerable. The posterior transverse impression is deep in all members of all species, narrow in members of most, broad in those of a few. Shape of the impression varies within some species and between others from straight (Fig. 100) to anteriorly deflected medially (Fig. 111). In macrosculpture, the posterior impression ranges from smooth to punctate among members of different species, with intraspecific variation slight. The median longitudinal impression also varies in depth (from very shallow [Fig. 106] to moderately deep [Fig. 94]) and macrosculpture. The impression is either smooth or faintly rugulose in members of all species. In most members of most species, the impression is defined only between the anterior and posterior transverse impressions (Fig. 99); but in some members of most species (and most members of _N. ingens_) it is extended toward or to the apical and basal margins (Fig. 117). The basal foveae are linear in members of all species and either continuous laterally with the basal portion of the lateral groove (Fig. 86) or separated from the latter by a faint (Fig. 92) or more markedly developed (Fig. 84) convexity. The foveae are deep in members of all species (except _N. lyelli_ [Fig. 94]) but varied among species in width (from narrow [Fig. 94] to very broad [Fig. 101]). _Nebria virescens_ is unique in

that most of its members have two longitudinal grooves etched in the foveae, separated by a weak convexity (Fig. 84). Members of all other species have a single longitudinal groove in the foveae and no similar convexity (Fig. 87). The foveae are weakly divergent posteriorly (Fig. 118) in members of most species, approximately parallel (Fig. 87) or more markedly divergent (Fig. 111) in those of a few species. They terminate anteriorly at the posterior transverse impression (Fig. 84) in most members of most species, but are extended slightly on the disc (Fig. 96) in all members of a few species and few members of others. Interspecific variation in foveal macrosculpture is from smooth to vaguely rugulose or punctate. Most characters mentioned above for the foveae and pronotal impressions have been useful in distinguishing among closely related species or subspecies, less useful in comparisons of more distantly related forms.

A maximum of two pairs of setae are on the pronotum among Nearctic Nebria, and members of all species have at least one pair. The basolateral seta (Fig. 82) is positioned on the lateral margination at the basal angle and is present in members of all species except N. kincaidi Schwarz (Fig. 112) and N. carri n. sp. (Fig. 111). Presence (Fig. 84) or absence (Fig. 106) of the mid-lateral seta is an extremely important character in studying Nebria. I have seen no single example of intraspecific variation in its occurrence among the many thousands of specimens studied. Relative position of the seta is apparently constant, but some interpopulational variation is evident in N. lacustris. Members of N. nivalis have a short, arcuate, longitudinal tubercle medial to the insertion of the mid-lateral seta (Fig. 89). Closely related Asian species have a similar tubercle, but it is seen in

members of no other Nearctic species. Presence of the tubercle appears to be related to a slight lateral displacement of the seta; and the tubercle may be an enlarged and medially-displaced derivative of the lateral margination at that point.

Venter

Macrosculpture is reduced or absent from the prothoracic venter in members of Nearctic species. The prosternum, proepisternum and proepimeron are smooth in most members of most species. A few members of most species and all members of a few others (e.g. *N. gouleti* n. sp.) have the prosternum faintly punctulate or punctate anteriorly and laterally (Figs. 123 - 124). Members of a few of these same species also have the proepisternum faintly punctulate or punctate anteriorly (Fig. 123), and members of still fewer species also have similar faint macrosculpture on the proepimeron. In contrast, members of several Palaearctic species have coarse punctation on the ventral prothoracic sclerites.

The prosternal intercoxal process is lanceolate (Fig. 126) or sublanceolate (Fig. 125A) in members of Nearctic species. Very little intraspecific variation in shape was observed; and interspecific differences in shape of the apex and relative width of the base were, therefore, quite obvious. Shape of the process in members of *N. appalachia* (Fig. 127) is unique. In members of all other species, the base of the process is much narrower than more apical regions. The process itself is smooth (without macrosculpture) and glabrous ventrally in all Nearctic species. Interspecific variation in margination of the process is apparent. In members of some species,

margination is restricted to the basal region (anterior to or at the level of the front coxae) (Figs. 130 - 131). Members of other species have the process with complete margination (Fig. 125) or with only the apex unmargined (Fig. 127), while those of a few species have the margination interrupted for a short distance basally (Fig. 132) independent of the extent of margination apically.

The front coxal cavities are basally open (not closed posteriorly by contact of the proepimeron with the prosternal intercoxal process) (Fig. 133), uniperforate ("unbridged" of Bell, 1967) internally, and confluent medially (dorsal to the intercoxal process (Fig. 134).

3.214 Pterothorax

Dorsum

The scutellum (i.e. mesoscutellum) is visible in all nebriines as a small triangular sclerite wedged between the basimedial angles of the elytra and base of the pronotum (Fig. 1). Other dorsal sclerites of the pterothorax are obscured by the base of the pronotum and/or the elytra and were not examined comparatively.

Elytra

The elytra are moderately convex in members of most species, slightly flat dorsally or more strongly convex in those of a few species. All nebriines lack elytral pubescence.

Elytral silhouette (outline shape of the elytra taken as a unit) (Figs. 135 - 143) contributes substantially to habitus; and differences observed grossly are often more apparent than real. Because in comparing elytral shape among intact specimens both elytra are normally viewed at once (halves of a whole), the visual effect of slight

differences in the shape of one elytron is doubled. Nonetheless, differences in silhouette are extremely useful in distinguishing taxa. Among members of Nearctic species, the following shapes are seen: (1) rectangular (Fig. 135), with lateral margins approximately parallel and width across the base about as broad as the greatest elytral width; (2) subrectangular (Fig. 136), with lateral margins slightly rounded and base broad; (3) subovoid (Fig. 137), with lateral margins moderately rounded and base slightly narrowed; (4) subovoid-narrowed (Fig. 138), similar to subovoid but with elytra narrowed sub-basally also and lateral margins approximately straight in the basal half; (5) ovoid (Fig. 139), with lateral margins markedly rounded and base narrowed; and (6) tear-shaped (Fig. 140), similar to ovoid but with elytra markedly narrowed basally and sub-basally. Components of elytral shape (including width of base, shape of lateral margins, shape of humeri, etc. [see below]) are markedly correlated with size of the metathoracic wing (see section 4.41 for discussion).

Study of the elytra singly (i.e. one elytron) provides numerous useful characters, a few recognizable as components of gross shape (silhouette) as discussed above. Detailed comparisons using these characters provide much more specific information than does silhouette alone. Terms used in reference to the elytron are illustrated in Fig. 146 . As noted above, width of the elytral base (distance from the scutellum to the humerus) is varied among members of different taxa, ranging from broad (Fig. 153) to very narrow, reaching an extreme in members of _N. kincaidi kincaidi_ Schwarz (Fig. 149). The basal margination of the elytron is varied in form and shape. It is smooth

(Fig. 150) or wavy (Fig. 149), and, except in a few taxa, both forms are found among members of the same taxon. The margination may be straight or very weakly concave anteriorly (Fig. 153) or moderately (Fig. 150) or markedly (Fig. 149) so. The lateral terminus of the margination (i.e. at the humeral angle) is directly opposite the medial terminus (i.e. at or near the scutellum) (Fig. 153) or displaced anteriorly (Fig. 148) or posteriorly (Fig. 154). Distinction should be made here between the humerus itself (the laterobasal corner of the elytron) and the humeral angle (as I use the term, referring to the angle, if any, formed by the juncture of the lateral groove and basal margination of the elytron). Development of the humerus differs markedly among members of some different species and/or subspecies. It is rectangular (rounded apically only) (Fig. 153) or slightly (Fig. 152) to strongly (Fig. 154) rounded, or, at an extreme, flattened and essentially absent (Fig. 149). The apex of the humerus is smoothly rounded (Fig. 153), faintly (Fig. 158) or markedly (Fig. 157) carinate and anteriorly projected or, as in some members of _N. virescens_, slightly denticulate (Fig. 155). The humeral angle does or does not mirror the humerus itself. For example, the angle is markedly defined while the humerus is rounded (Fig. 149) in members of some species or rounded (therefore absent) with a rounded humerus (Fig. 154) in those of other taxa. A subhumeral sinuation in the lateral margin (Fig. 146) is present in members of most species but absent from (Fig. 150) or more markedly developed in members of a few. All members of all species have a subapical sinuation of the margin (Fig. 146), more markedly developed than the subhumeral sinuation. The subapical sinuation is associated with the apical

terminus of the internal elytral plica (see below). Interspecific differences in width of the lateral elytral explanation are slight but consistent, ranging among members of different species from narrow (Fig. 155) to relatively broad (Fig. 160). The explanation, delimited medially by the lateral groove, is clearly narrowed basally in members of most species. A subapical carina is present, in all nebriines examined, at the confluence of the fourth through seventh elytral intervals (Fig. 146). Among Nearctic Nebria, it varies in degree, from slightly to markedly developed, and length (moderate [Fig. 159] to long [Fig. 160]). Both development and length of the carina appear to correlate with depth of the subapical sinuation (i.e. increased development with increase in the subapical sinuation depth).

Shape of the elytral apices is another useful character. In most other nebriines and in members of some Nearctic species, the apices are narrowly rounded laterally, straight and closely approximated along the sutural (medial) margin (Fig. 163). In members of other species, the apices are: (1) broadly rounded apically, slightly arcuate and divergent medially (Fig. 167); (2) obliquely blunted apically and slightly divergent medially (Fig. 166); (3) broadened and obliquely blunted apically, slightly divergent medially (Fig. 164); (4) slightly pointed apically, arcuate and more widely divergent medially (Fig. 162); (5) broadly blunted apically and widely divergent medially (Fig. 168); or (6) slightly pointed apically and sinuate and divergent medially (Fig. 165). Intraspecific variation in this character is slight.

In members of all species, the internal plica of the elytron (Figs. 169 - 170) is longitudinal, simple, keel-like, just extended to

but not across the epipleural margin at the subapical sinuation of the lateral margin. The plica is demarcated externally (dorsally) by the lateral groove. The elytral locking mechanism in Nebria species is therefore, relatively simple. With the elytra in folded (closed) position, the dorsomedial edges of the abdominal sterna (see also below) appear to fit between the elytral epipleuron and the internal plica (Fig. 170), most securely so just anterior to the juncture of these two flanges (i.e. at the elytral margin).

In members of all Nebria species, each elytron bears eight complete striae, the "first" through "eighth" (beginning medially), and one abbreviated stria, the "scutellar striole", medial to the base of the first complete stria (Fig. 146). Interspecific variation in depth of impression and punctuation of the striae is evident. In members of most species, striae are moderately impressed, deeply impressed in members of several species and weakly so in those of only a few species. In N. virescens (Fig. 155) and N. suturalis (Fig. 159), all and some members, respectively, have the lateral striae much more weakly impressed than the medial three or four striae. Nearctic Nebria, compared with members of several Palaearctic species, have only weak punctuation of the striae. Among members of Nearctic species, striae range from faintly punctulate to evidently (but slightly) punctate. Density of punctation ranges from moderate to sparse (again compared with the Palaearctic Nebria).

Elytra, and especially the basal regions of same, are among those parts of beetles most commonly preserved as fossils. In my attempts to distinguish the elytra of Nebria specimens from those of other carabids of similar size in samples sent to me for identification, the most

useful characters found were (1) branching pattern of the first and second striae, and (2) relationship between the first stria and the scutellar striole. In all members of most nebriine species, and at least in some members of all species, first and second striae branch from a common stem at some distance from the basal margination (Fig. 171). In all nebriines, the scutellar striole is free, not joined distally with the first stria. All _Pterostichus_ (Fig. 174) and _Amara_ (Fig. 175) specimens examined agreed with nebriines in the branching pattern of first and second striae; but in members of each of these other genera, the scutellar striole either joins or crosses the first stria distally. Specimens of _Diplous_ and _Patrobus_ species agree with nebriines in both characters, except that they lack a basal margination (Fig. 177). In all _Agonum_ specimens examined, the first and second striae arise separately from the basal margination (Fig. 176). In the _Nebria_ individuals noted as exceptions above, first and second striae arise either separately (Fig. 173), as in _Agonum_ specimens, or from a common point on the margination (Fig. 172). In all such exceptional _Nebria_ individuals, fortunately, the elytral intervals are at least weakly catenate (see below), thus permitting recognition of the specimen as a _Nebria_. Individuals representing _Nebria_ species are distinguished from those of _Pelophila_ and _Leistus_ (i.e. other nebriines), respectively, by the abbreviated scutellar striole (complete in _Pelophila_ members) and the faint and sparse punctation of the striae (relatively coarse and dense in Nearctic _Leistus_ members).

Characters of the elytral intervals are also useful in

distinguishing and relating taxa. Range in topography of the intervals among members of different Nearctic species is from flat to markedly convex. Intraspecific variation in topography is low in most species, but geographically correlated in some. All intervals are smooth (i.e. without macrosculpture) and approximately equal in width in members of all Nearctic taxa, continuous (uninterrupted) in members of several species. In members of many species, however, third, fifth and seventh intervals (singly or in various combinations, depending on the taxon) are interrupted by moderately (Fig. 156) to very markedly (Fig. 161) developed setiferous foveae. A number of fixed setae are present on these and certain other intervals. Conspicuous interspecific differences are in the presence and number of these setae and in modification of the intervals associated with their sockets. A single seta, the presence of which is most simply noted by reference to its socket (the "basal pore"), is found near the elytral base on the first interval between the first stria and the scutellar striole (Fig. 146). It is present in all members of most species and most members of others, but it is absent from all members of a few species. Lindroth's (1961:65) use of the presence of the basal pore as a key character was unfortunate because of the intraspecific variation in several species. Members of all species have one or more setae on the third interval, with a maximum of 10 in individuals of several species. Members of several species also have one or more setae on the fifth and/or seventh intervals (with a maximum of nine for each interval in some individuals of some species). Intraspecific variation in the numbers of setae on each of these intervals is very great; and presence of

setae on an interval rather than their number appears to be the more reliable character in general. Continuity of the intervals is determined by development of setiferous pores (sockets). Intervals appear continuous (uninterrupted) if setae are absent (Fig. 157) or if setiferous pores are minute (Fig. 155) or slightly (Fig. 158) to moderately (Fig. 159) foveate (i.e. the foveae are shallow, with diameter less than or equal to the width of the interval). If the foveae are deep and broader than the interval and adjacent striae are slightly to moderately distorted locally, the interval is 'catenate' (Fig. 160). In members of species with markedly convex intervals (e.g. Nebria schwarzi Van Dyke), the catenations (if present) are quite spectacular, the deeply foveate setiferous pores punctuating short, tuberculate sections of interval, providing a visual affect similar to a 'chain of beads' (Fig. 161).

Setae on ninth elytral interval, form the umbilicate series. These are numerous (Fig. 156), ranging among members of different Nearctic species from eight to 19 in number. There is no apparent separation of the setae into groups (such as anterior or posterior groups noted in some carabids by Jeannel [1925]). Intraspecific variation in number of setae in the series is too great to permit useful interspecific comparisons. The first (most basal) seta of the series in members of N. virescens is unique in position (Fig. 155), relatively remote from the humeral angle. In members of other Nearctic species, the first seta is much closer to the base (Fig. 156).

Wings

Among members of Nearctic Nebria species, relative size and shape of the hind (metathoracic) wings (Figs. 181 - 195) vary markedly between and within species. Wings are either reduced in length and/or width or full-sized (Fig. 182)-- that is, long, with an acute, reflexed apex distal to the stigma (see Fig. 181), broadly membranous posteriorly and with a full venation pattern (see below). Several intermediate stages in a hypothetical transition from macroptery (presence of full-sized wings) to aptery (complete absence of wings) are identified among members of one or another Nearctic species with wings of reduced size. The stages (character states) are: (1) complete miniature (Fig. 183)-- the wing is identical in shape and venation to a full-sized wing but slightly smaller relative to body size of the individual; (2) narrowed/slightly shortened (Fig. 184)-- wing length is slightly reduced (complete reflexed apex is present), the membranous posterior region is reduced, decreasing overall width, but venation is essentially complete; (3) broad/truncate (Fig. 185)-- the wing is unmodified basally but abruptly truncate just distal to the stigma; (4) narrowed/truncate (Fig. 186)-- the wing is truncate as in (3) above, also narrowed as in (2) above, and with venation essentially unmodified; (5) 'brachypterous' (Fig. 187)-- the wing is considerably reduced in length and width (and slightly in venation of the posterior margin), but with the apex pointed and reflexed distal to the stigma; (6) 'micropterous' (Fig. 188)-- the wing is considerably reduced in length, width and venation but with a stigma evident (although displaced proximally in members of some taxa); (7) 'advanced

micropterous' (Fig. 189)-- the wing vestige appears vaguely wing-like, with some venation of the basal area evident; and (8) strap-like (Fig. 190)-- the wing vestige is very short, slender and lobate, with one or two veins still evident but highly distorted.

Interpopulational (i.e. geographical) variation in wing development is exhibited by several species. Intrapopulational variation, however, is restricted to a very few taxa; and among members of these taxa, variation is continuous (from one character state to another, with intermediates also found) rather than discrete (di- or polymorphic). Such classic examples of wing dimorphism as those discussed by Lindroth (1945-49, 1963a, 1963b, 1969a and 1969c) and Darlington (1936 and 1943) are not, apparently, repeated in Nearctic Nebria species. See section 3.234 for comments on relationship between wing size and dispersal capability and section 4.41 for discussion of the structural modifications associated with wing reduction.

Folding pattern of the wing in Nebria was discussed by Forbes (1926) and is similar among members of all Nearctic species with full-sized wings. Reduction in wing size is accompanied by divergence from the basic folding pattern through simplification. 'Advanced micropterous' and 'strap-like' wing vestiges have no transverse folds.

The venation pattern basic to all Nearctic Nebria species with fully-winged members is illustrated in Fig. 181. Terms used are those of R. D. Ward (unpublished manuscript) and generally consistent with those of Hamilton(1972). As noted by Chiolino (1970), proper interpretation of venation patterns on other than full-sized wings is difficult or, when wings are markedly reduced, impossible. I have,

therefore, studied venation only of macropterous individuals. Among these, intraspecific variation in presence, continuity and position of various veins, cross-veins and cells is slight but surprisingly frequent, precluding reliable interspecific comparisons in many instances. Shape of the oblongum cell (0) and its relationship to the Cubitus Vein (Cu) varies slightly but consistently among members of different taxa. In members of all Nebria species sampled, the two median cubital (m-cu) cross-veins forming the cell join posteriorly at an acute angle. Interspecific and/or intersubspecific variation in this angle is observed (Figs. 197 - 205), due mainly to the degree to which the junction of the distal m-cu cross-vein with the Cu Vein is displaced proximally (toward the wing base). As a result, the 0 cell is subquadrate (clearly four-sided) (Fig. 197), or approximately triangular (Fig. 198), or intermediate in shape between these extremes (Fig. 182). Additional variation among taxa is seen in position of the junction of m-cu cross-veins. In members of some taxa, the junction is at the Cu Vein (Fig. 197); but in those of other taxa, the junction (and, therefore, the 0 cell itself) is slightly (Fig. 199) to quite (Fig. 200) removed from the Cu Vein and joined to it by a narrow stalk (the fused m-cu cross-veins). Surprising intraspecific variation is seen in the shape and occurrence of the wedge cell (W); but in every instance, most members of the taxon involved demonstrated the typical character state (Fig. 181). Variants seen included: (1) a W cell lacking the empusal-anal cross-vein proximally (Fig. 203), in some members of several taxa; (2) a doubled W cell (Fig. 201), in a few members of N. pallipes; and (3) a W cell open to the margin (Fig. 202),

in some members of a few taxa.

The sclerotized microtrichial field on the marginal cell between the P + Cu_2 and E_1 Veins in members of Trachypachus (Fig. 206), Amphizoa and of at least some dytiscids is lacking from Nebria members.

Venter

If present, punctation is restricted to the mesosternum (laterally only), mesepisternum, metasternum (laterally only) and metepisternum among members of Nearctic species. In members of many species all these sclerites are smooth, while among those of other taxa, range in macrosculpture is from weakly punctulate to moderately (but sparsely) punctate. In general, punctation of the mesepisternum is more strongly developed than that of other sclerites. In contrast to the above, members of several Palaearctic species exhibit relatively coarse punctation of the venter, including also the mesepimeron.

Interspecific variation in relative length of the metasternum (Figs. 207 - 210) is considerable, and intraspecific variation is low enough to make this a relatively useful character. Following Erwin (1970) and Erwin and Ball (1972), a measure of relative length was obtained by comparing longitudinal diameter of the right middle coxa with length of the metasternum (measured on a line centered on the right middle coxa center) (Fig. 207). Length of the metasternum was recorded as (1) clearly greater than (Fig. 208), or (2) approximately equal to (Fig. 209), or (3) clearly less than (Fig. 210) the diameter of the middle coxa. Metasterna in members of a few taxa are intermediate between these arbitrary character states and were so noted. Because relative metasternal length appears correlated with hind wing

length (refer to discussion in section 4.41; see also Erwin, 1970 and Erwin and Ball, 1972), taxa whose members display intermediate conditions in this character are expected; and their existence does not reduce the value of the character. Variation is also evident in extent of the margination of the anterior metasternal intercoxal process (i.e. between the middle coxa posteriorly) (Figs. 211 - 214). Margination is present basilaterally only (Fig. 211) or either faintly (Fig. 212) or distinctly (Fig. 213) present across the midline also (that is, complete).

3.215 Legs

Among members of Nearctic _Nebria_ species, legs are quite similar in general form, especially if compared with those of other carabids. Interspecific variation is conspicuous, however, in relative overall length and proportion. The legs of members of a few taxa are relatively short and robust (Fig. 217) or very long and slender (Fig. 218), while members of most taxa have moderately long and slender legs (Fig. 219). Males of all taxa sampled have relatively longer legs than conspecific females.

Coxae

The front (Fig. 220) and middle (Fig. 221) coxae are globose, the former asetose. The middle coxa is bisetose in all members of most species, with one anteriomedial and one anteriolateral seta apically. Some members of _N_. _metallica_ Fischer v. Waldheim, _N_. _schwarzi schwarzi_ Van Dyke and _N_. _spatulata_ Van Dyke have two anteromedial setae (Fig. 222); and in one of a few individuals of some other taxa two of

the medial and/or lateral setae were found. The hind coxa (Figs. 224 - 229) is flattened, transverse and laterally narrowed. The lateral portion, or "wing" (Lindroth, 1961), is divided by the transverse section of the coxal ridge (an extension of the lateral posteroventral margin of the expanded medial portion of the coxa). Lindroth noted that the posterior portion of the "wing" is flat (horizontal) in members of Pelophila species (Fig. 223) but vertical and obscured in ventral aspect by the flat and more ventrad anterior portion of the "wing" (Fig. 224) among Nebria members. However, some interspecific variation in the plane of the posterior portion is apparent among Nebria. In members of N. virescens (Fig. 225), the posterior portion is easily visible ventrally and its plane is clearly less than vertical (about 45 degrees from vertical). In members of all other Nebria sampled, the posterior portion is less visible (Fig. 226) or totally hidden (Fig. 224) and more nearly or completely vertical. Setae on the hind coxa are confined to the broad medial portion. Members of some species have a single basal seta (Fig. 225), but most members of most species have two or more (Fig. 224) (to a maximum of seven in some members of N. mannerheimii Fischer v. Waldheim). Inter- and intrapopulational variation in this character is considerable in some taxa. A single apical seta (Fig. 225) is found in all members of all species except N. schwarzi, in which almost all members have more than one seta (Figs. 226 - 227) (to a maximum of six).

Trochanters and femora

In members of all Nearctic species, the front (Fig. 230) and middle (Fig. 231) trochanters are roughly wedge-shaped, each with a

single apicoventral seta. The hind trochanter (Fig. 232) is lobate, weakly and roundly pointed apically and asetose. Femora are similar in members of all Nebria species sampled, the front femur (Fig. 233) slightly swollen dorsoventrally near its middle, the middle (Fig. 234) and hind (Fig. 235) femora approximately cylindrical, tubular.

Tibiae

In all nebriines studied, the anterior tibia (Fig. 236) has a simple, sulcate antennal cleaner ("Grade A" of Hlavac, 1971) occupying the distal 0.5 to 0.33 of its ventral surface. Insertion of both tibial spurs is apical; and although the apical tibial margin is moderately oblique, with the lateral (i.e. structurally posterior, or euposterior) margin slightly retracted proximad, the arrangement of spurs is essentially isochaetous (Jeannel, 1941; see also Bell, 1964 and 1967; Hlavac, 1971).

Interspecific variation is evident among members of Nearctic species in the topography and vestiture of the dorsal surface of the middle tibia (Figs. 237 - 240). The dorsal face is uniformly flat or slightly convex (Fig. 237) in all members of N. appalachia and N. pallipes and in some members of a few other taxa. In members of some other taxa, the face is moderately concave in its distal half (but not apically) (Fig. 238) ; but in those of most taxa, the face is broadly sulcate in its distal half, including the apex, as in N. virescens (Fig. 240), or not (Fig. 239). Slight intraspecific variation in linear extent of the concavity or sulcus is evident. The distal 0.33 to 0.5 of the dorsal face also bears numerous setae (Figs. 237 - 240) between the two dorsal longitudinal setal rows and situated in the

sulcus or concavity (if present). Together, the setae form a more or less dense brush, probably serving as a simple cleaning organ. The brush is well developed except in members of N. appalachia and N. pallipes.

The hind tibia is unmodified among Nearctic Nebria; but in members of the Palaearctic N. chalceola Bates and related taxa, the dorsal face of this tibia is also sulcate.

Tarsi

Characters of the tarsi have been used extensively in Nebria classification (Bänninger, 1925; Jeannel, 1937), especially in recognition of subgenera (which are not considered in this presentation). In the Nearctic fauna, however, interspecific variation in tarsal characters is generally slight and/or restricted to peculiarities in members of a few taxa.

The basal three tarsomeres (i.e. first through third tarsomeres) of the front tarsus are relatively broad (laterally expanded) (Fig. 242) in males of all species. With only two exceptions, the tarsomeres of the middle and hind legs in males and of all legs in females are slender. In N. ingens (Fig. 245) and some populations of N. ovipennis (Figs. 246a,246b), all tarsomeres of the front legs in males are relatively broad; and tarsomeres of the male middle and hind legs and all legs in females are also (but slightly less) broadened (Fig. 245) compared with those of members of other species. An additional feature unique to members of N. ingens is the excavation (concavity) of the ventral surfaces of the tarsomeres (Fig. 245), especially prominent on those of the middle and hind legs. These surfaces are slightly

convex or flat in members of all other taxa.

Again, with members of N. ingens and some populations of N. ovipennis as exceptions, males of all Nearctic species have pads of adhesive setae (Figs. 241 - 243) on the ventral surfaces of the first through third tarsomeres on the front legs. In some members of N. ovipennis (Figs. 243a,243b), the pads on all three tarsomeres are slightly or moderately reduced in area (number of hairs). In members of N. ingens (Fig. 242), the pad is absent from the third tarsomere, greatly and moderately reduced on the second and first tarsomeres, respectively. The other tarsi in males and all tarsi in females are without ventral pads of setae in all species.

The sparse dorsal pubescence on tarsi in members of numerous Palaearctic species of Nebria is lacking from members of Nearctic taxa, except for a few members of N. diversa LeConte. Tarsomeres of the hind tarsus in members of N. superna Andrewes and a few other Palaearctic species are distinctly compressed basally; but these are quite cylindrical in members of all Nearctic species.

Interspecific variation in shape of the ventro-apical margin and length and position of associated setae on fourth tarsomere of the hind tarsus is quite conspicuous. In members of N. virescens (Fig. 249), the ventro-apical margin is truncate and the ventro-apical setae are approximately symmetrical in length and position. In members of all other Nearctic species, the margin is asymmetrical, either weakly (Fig. 250) or more strongly (Figs. 251 - 252) lobate ventro-laterally (i.e. anatomically anteriorly, or euanteriorly). Associated with development of this projected ventral lobe is increased asymmetry in

length, position and number of the ventro-apical setae (Figs. 249 - 252).

Tarsal claws are similar in members of all species-- simple, evenly arcuate and equal in length. Slight interspecific variation in length and thickness of the claws was observed but not analyzed.

3.216 Abdomen

Dorsum

The dorsum of the abdomen, including tergal and pleural regions, is completely obscured by the elytra and is, therefore, unavailable for study except after removal or displacement of the elytra and hind wings. A brief survey of dorsal structures among members of selected taxa revealed few differences. Detailed comparative study of dorsal abdominal structure was, therefore, deleted except for those structures associated with the genitalia and/or ovipositor (see below).

Venter

The abdominal sterna (Figs. 253 - 259) are, in general, without punctation or other macrosculpture. However, the first visible sternum (divided medially by the hind coxae into two small, lateral triangular sclerites), although smooth in all members of some species and some members of others, is faintly punctate or punctulate in all or some members of most Nearctic species. All sterna bear a pair of broad lateral pits (Fig. 253). In members of most taxa, the pits are most markedly developed on the first visible sternum, least so on the second. Some interspecific variation in depth and distinctiveness of the pits was observed.

The sterna are carinate dorsolaterally, the basal five (visible) sterna broadly deflected dorsomedially from the carina, the last visible sternum (that is, the sixth, or "anal" sternum) narrowly deflected basally and not at all apically (Fig. 254). The narrowed portion of the deflected area of the last sternum apposes the subapical sinuation of the elytron. Refer to the section on elytral structure above for brief comment on the elytral locking mechanism involving the sterna.

The second visible sternum is glabrous in members of most taxa; but in _N. hudsonica_ and _N. gouleti_ n. sp. (Fig. 255), all but a few members have a patch of setae medially between the hind coxae. In some members of _N. ovipennis_ and related species, either a single pair of paramedial setae or a small number of scattered setae is present in the same region on this and (in fewer individuals) also on the third visible sternum. On the third, fourth and fifth visible sterna, a single pair of posterior paramedial ("ambulatory") setae (Fig. 257) is found in members of some species; but in those of most taxa, two or more (to a maximum of eight) pairs of these setae are present (Figs. 255, 258). One or more (to a maximum of 15) pairs of anterior paralateral setae are found in members of some species (Fig. 258); but these are absent from members of most taxa (Fig.253). On the "anal" (sixth visible) sternum, two or more pairs of posterior paramedial setae (known on this sternum as the "anal setae") are present in both males and females of some species (Figs. 258 - 259). In most species, however, a single pair is present in males, two or more pair in females (Figs. 255 - 256). The usefulness of this character is somewhat

diminished, however,by the relatively frequent occurrence of individuals apparently atypical of their respective taxa in the character.

3.217 Male genitalia

Lindroth (1961a:61) noted that"the organization of the ♂ genitalia [in Nebria] is so simple, with no chitinized structures in the internal sac of [the] penis, that it is less useful than in most other genera". In spite of this overall structural simplicity and similarity, differences in shapes of one or more genitalic structures are recognized between members of almost any two taxa (i.e. species and/or subspecies). Intraspecific and intrapopulational variation in form and structure are slight but significant enough to require relatively large samples to insure valid comparisons among taxa. Differences among males of different species groups are relatively great; and, in most instances, male genitalic characters are at least as valuable in demonstrating relationship among species as in distinguishing them.

Male gentalia (Figs. 260 - 298) include the following parts (Fig. 260): the median lobe, comprised of a basal bulb, shaft, apex, and eversible internal sac which bears the gonopore; two parameres ("lateral lobes" of Sharp and Muir, 1912), each lateral to the median lobe and attached to the ventrolateral corner of the basal bulb of the latter; a 'dorsobasal sclerite'; and the modified sclerites of segment 9. Structural differences in each of these parts have been found among Nearctic Nebria. Orientation of the genitalia in the following discussion is in copulatory position (Fig. 261). In fact, however, this position represents a rotation of 180 degrees to the left for the median lobe and parameres relative to the primitive coleopteran

orientation. In repose, these structures lie on the (primitive) left side (rotated 90 degrees left) and rotate an additional 90 degrees left on eversion for copulation (see Jeannel, 1926).

Median lobe

Among all nebriines studied, the median lobe is complete (closed) dorsally. In members of all but one Nearctic species, the basal bulb is large, roughly rectangular in lateral aspect, with the basal orifice broadly open (occupying the entire base) (Fig. 264). Males of *N. virescens*, however, have the bulb slightly smaller, rounded dorsobasally, and with the basal orifice small and restricted to the ventral portion of the base (Fig. 262). In males of *N. brevicollis* (Fabricius) (Fig. 263) and several other Palaearctic species, the bulb is large and broadly open basally, but more triangular, wedge-shaped, in lateral aspect.

There are interspecific differences in several characters of the shaft of the median lobe. One such character is the angle to which the axis of the shaft is bent (Fig. 260). In males of all *Nebria* species sampled, the axis is bent at least 90 degrees (Fig. 264), in males of some species as much as 140 degrees. To simplify comparisons and further discussion, the shaft is divided into two portions (Fig. 260): (1) a basal portion, here called the 'mid-shaft', delimited by the basal bulb basally and the basal margin of the apical orifice apically; and (2) an apical portion, here called the 'preapical-shaft', delimited by the basal and apical borders of the apical orifice. Among males of different species, the 'mid-shaft' ranges in thickness (lateral aspect) from very slender (Fig. 263) to very broad (Fig. 278). Interspecific

variation in taper of the 'mid-shaft' is considerable. In males of different taxa it is cylindrical (i.e. of approximately equal width throughout) (Fig. 264) or moderately to markedly tapered either apically (Figs. 263 - 273) or basally (Figs. 281 - 285). Cross-sectional shape of the 'mid-shaft' also differs among species. In males of most species, it is weakly to moderately compressed (Fig. 268); but in members of a few others, it is either markedly compressed (Fig. 275) or circular (Fig. 264). In males of _N. ovipennis_ (Fig. 280) and related species, the right lateral wall of the 'mid-shaft' is locally invaginated to form a small pouch (directed basad and open toward the apex) (see also Erwin and Ball, 1972). The pouch is unique to males of these few species but varies among them in depth and precise configuration.

The 'preapical-shaft' bears the apical orifice, through which the internal sac is everted during copulation. In part, shape characteristics of this part of the shaft are simply a continuation of those of the 'mid-shaft' (e.g. thickness and taper). Independent characters of the 'preapical-shaft' include its length and shape (in lateral, dorsal and apical aspects) and the resulting plane of the apical orifice. All these characters vary considerably interspecifically. In members of some taxa, the 'preapical-shaft' (lateral aspect) is long, with its dorsal margin (outer curvature), and therefore plane of the apical orifice, longitudinal (Fig. 263). In males of other taxa, it is shorter (Figs. 265 - 285), with its dorsal margin weakly (Fig. 265) to moderately (Fig. 275) oblique and apically convergent with the ventral margin (inner curvature). The plane of the apical orifice in

these adults faces apicodorsally rather than directly dorsad. The extreme example of the short and oblique condition is seen in males of Colorado populations of N. trifaria trifaria LeConte (Fig. 283). Both shortness and obliqueness are, in males of most taxa, associated with a basally tapered (i.e. apically expanded) 'mid-shaft'. Among males of different taxa, shape of the ventral margin ranges from smoothly arcuate (Fig. 264) to weakly but abruptly deflected ventrally (Fig. 267) or weakly (Fig. 265) to strongly recurved (Fig. 274). Comparisons of the shape of dorsal margin of the 'preapical-shaft' and plane of the apical orifice are complicated by the fact that interspecific differences in symmetry (i.e. shape in apical (euposterior) and dorsal aspects) are also evident. In males of a few taxa (e.g. N. gouleti n. sp., Fig. 286), the dorsal and ventral margins of the 'preapical-shaft' are bilaterally symmetrical (in apical aspect); but in males of most taxa, the shaft is moderately (Fig. 272) to markedly (Fig. 279) oblique (or twisted) and depressed. The plane of the apical orifice, independent of its orientation in lateral aspect, faces dorsad and right laterad in these beetles rather than directly dorsad. In males of some taxa, the'preapical-shaft' is, in dorsal aspect, symmetrical and narrowly (Fig. 286) or more broadly (Fig. 275) tapered, or asymmetrically tapered toward the right (Fig. 287) or left (Fig. 285). Males of other taxa have the lateral margins approximately parallel (Fig. 267) or weakly divergent apically (Fig. 262).

The apex of the median lobe, here defined as that part distal to the apical margin of the apical orifice, exhibits great interspecific

and some interpopulational variation in shape. Differences in shape of the apex are, in many instances, alone sufficient for distinguishing members of different taxa. In dorsal aspect, range in shape among males of Nearctic species is from narrow and sharply pointed apically (Fig. 286) to broad, spade-like and rounded apically (Fig. 262), with numerous intermediate shapes also seen (e.g. Figs. 267, 275). Differences in symmetry are also evident in dorsal aspect among males of different taxa, ranging from symmetrical (Fig. 286) to deflected right (Fig. 268) or left (Fig. 284). In each instance, symmetry of the apex reflects symmetry trends initiated in the 'preapical-shaft' (see above). In apical (i.e. euposterior) aspect, the apex is depressed (flattened) and its apical margin horizontal in males of _N. virescens_ (Fig. 262). In males of all other Nearctic taxa, the apex is compressed and its apical margin either vertical (Fig. 286) or moderately (Fig. 281) to strongly (Fig. 275) oblique (rotated) left. In lateral aspect, the apex ranges in length from very short (Fig. 283) to elongate (Fig. 282), with examples of both extremes among males of different subspecies of _N. trifaria_ LeConte. Differences in shape and direction of the apex in lateral aspect are also striking. Range in shape is from narrow and sharply pointed (Fig. 286) to broadly rounded (Fig. 284) or hooked (Fig. 278). In males of most taxa, the apex is a straight or smoothly arcuate extension of the shaft (Fig. 286); but in males of some taxa, it is deflected dorsally (Fig. 282) or ventrally (Fig. 267) from the arc of the shaft or faintly recurved at its base (Fig. 266).

As noted above, detailed comparative study of the form and

structure of the internal sac was deferred, pending development of an effective technique for full eversion and inflation of the sac. [Such a technique, developed by T. Gruenwald (Adelphi, Maryland), is now available (personal communication) and will be used in subsequent studies on Nebriini]. However, a brief survey of the internal sac among members of the Nearctic fauna indicates that marked interspecific differences exist in its shape (including length, symmetry and the number and arrangement of lobes). Figs. 288 and 289 present examples of two different sacs. In all males, the sac is membranous, without teeth, spines, hooks or plates seen in members of many other carabid genera. Microtrichial fields are evident, however; and while their position and number have not yet been studied, interspecific differences in these potential characters are probable.

Parameres

The parameres of males of all nebriine taxa sampled are asetose. Nebria virescens males have the parameres approximately symmetrical in length and shape (Figs. 290 - 291); but in males of all other Nearctic taxa, the parameres are asymmetrical (i.e. differ in both characters) (Fig. 294), with the right paramere longer than the left. Interspecific and interpopulational differences in shape and relative lengths of each paramere are evident, at least in some taxa. The left paramere is spatulate (short, broad, apically blunted) (Fig. 293) in males of most species, short and narrow (Fig. 291A) in males of a few, and broad, relatively elongate and acuminate (Fig. 295) in males of other taxa. The right paramere is very long, slender and arcuate (similar in arc to the median lobe) (Fig. 292) in males of all taxa

except N. virescens, in males of which it is short, spatulate and similar to the left paramere. Of some interest (but unknown homology and significance) is a vague to heavily sclerotized strap-like sclerite in the medial membrane of the right paramere in males of certain species (e.g. N. schwarzi) (Fig. 296). The sclerite, here termed the 'right medial parameric sclerite', articulates with neither the paramere nor the median lobe and appears to be simply a strengthened region of the medial membrane.

'Dorsobasal sclerite'

I use the term 'dorsobasal sclerite' to refer to structures (Figs. 262 - 265) located dorsobasally and associated with the basal bulb of the median lobe in members of Nearctic Nebria. There are considerable differences in the shape and position of this 'sclerite' among taxa and great variation in degree of its sclerotization within taxa. In males of N. virescens, it is well-sclerotized and positioned dorsobasally as a mid-sagittal crest or fin (Fig. 262). In males of all other Nearctic Nebria, the 'sclerite' (if homologous with the crest described above) forms a thin, flat collar around the dorsal and lateral surfaces of the basal bulb (Fig. 260). In some males of many taxa, it is very weakly sclerotized and difficult to see. The membrane bearing the 'sclerite' is attached to the margin of the basal orifice of the median lobe; and in some specimens in which the genitalia have been forcibly everted, the sclerite is seen in extended position, basal to the median lobe itself (Fig. 263).

The homology of this 'sclerite' is uncertain; but it may represent a remnant of the "basal piece" (pars basalis) seen in some Adephaga and in many other Coleoptera. The basal piece is usually described as

absent or membranous among Carabidae (Ball, 1960).

Sclerites of ninth abdominal segment

The sclerotized remains of the ninth abdominal segment (the "genital segment", or "urite X" of Jeannel, 1941) in nebriines comprise the so-called "ring sclerite" and associated structures. Enclosed within the ring are the other genitalic structures described above. Shape of the ring differs slightly among members of nebriine taxa examined; but comparisons using shape characters appear to be useful only at the generic and subgeneric levels. Among Nearctic Nebria, structure of the ring is as follows (Figs. 297 - 298). The posterodorsal portion of the ring corresponds to the ninth tergum (with the anal opening immediately ventral). The tergum is narrow and entire (not divided medially), with the apical margin weakly convex and minutely notched near the left margin (for the opening of the left pygidial defense gland). The remainder of the sclerotized ring loops anteroventrally into the abdominal cavity from the basolateral corners of the ninth tergum. The homology of this portion of the ring is uncertain; but Edwards (1951) identified this structure in Amphizoa specimens as the ventrally fused ninth pleura. Distinctly separate apodemes are present on the tergum in Amphizoa specimens (Fig. 299), suggesting that the loop is not formed from distally-fused tergal apodemes. Articulating ventrally with the right basolateral corner of the ninth tergum is a triangular, partially-sclerotized pouch (Fig. 298) which serves as a sheath for the apex of the median lobe in repose. Homology of this structure is also uncertain; but Edwards identified a similar but more medial and symmetrical structure in

Amphizoa specimens (Fig. 299) as the ninth sternum.

3.218 Female genitalia

To date, the only comparative study of female genitalia among nebriines has been that of Erwin and Ball (1972) on the sclerites of the bursa copulatrix in members of the *trifaria* group (in the sense of these authors) of *Nebria*. My own review of female genitalic structure among nebriines and other carabids has revealed differences among various tribes, genera, species and populations in one or more characters. In the present study, 61 female genitalic characters were recognized and used in comparing nebriine taxa, 23 of these represented by a single characters state among members of the Nearctic *Nebria* fauna. Many of these characters have been extremely useful in reconstructing phylogenetic relationships among taxa (see section 4.1 below), thoroughly justifying the time and effort required in dissection and preparation of specimens prior to their study.

The female genitalia (Figs. 300 - 353) include the following parts: ovipositor (in a broad sense), comprised of the modified eighth sternum, proctiger, two paraprocts, two valvifers, paired remnants of the tenth sternum and paired coxostyli; bursa copulatrix; spermatheca; and spermathecal duct. Terms used for parts of the ovipositor approximate those of Tanner (1927). In a recent comprehensive review of the terminalia of terrestrial Adephaga (including an extensive study of musculature), Bils (1976) has suggested radically different segmental relationships of these parts. I choose to follow Tanner here to facilitate possible intergroup comparisons through the existing

literature on other carabids but mention Bils' equivalent terms for each part as well.

Eighth sternum

The eighth abdominal sternum ("coxosternum VIII" of Bils)(Figs. 300 - 304) is split medially into two halves, or hemisterna. These hemisterna lack pubescence; but in all nebriine females sampled, a fringe of setae traverses the medial one-third of the apical margin of each (Fig. 301). Interspecific variation is seen in both density and length of the fringe setae (Figs. 300 - 304). Among Nearctic *Nebria* females, the basal apodeme of each hemisternum is moderately long and wide (Fig. 301) (at least basally), with its apex deeply emarginate (Fig. 302), forming two separate heads. In females of a few taxa, the two heads are of equal length (Fig. 302); but in those of most taxa, the lateral head is slightly (Fig. 303) to much (Fig. 304) shorter than the medial head, with an extreme example seen in females of *N. virescens* (Fig. 300). The apodeme is flat and uniformly thin in all nebriines, without a thickened rod-like longitudinal reinforcement characteristic of Hydradephaga and females of *Trachypachus* (Fig. 304A) and a few other carabid groups.

Proctiger

The proctiger ("fused terga IX and X", Bils; see his "Abb. 20") (Figs. 305 - 306) is heavily sclerotized (at least basally) and glabrous in females of all Nearctic *Nebria*. It is hemispheric, apically convex and completely sclerotized (Fig. 306) in females of all taxa except *N. virescens*, females of which have the apical portion membranous (Fig. 305).

I see no reason to conclude that terga IX and X (*sensu* Bils) are fused in nebriines as he suggests, because structures very similar (in location and musculature) to that labelled "T.IX" in his "Abb. 6" (p. 166) for *Trachypachus holmbergi* Mannerheim are present also in nebriines (i.e. as the paraprocts of Tanner, 1927). The proctiger would,therefore, be tergum X alone.

Paraprocts

The paired paraprocts (Figs. 305 - 308) (equivalent to the remnants of "tergum IX" in *Trachypachus* specimens ["T.IX" in "Abb. 6", p. 166] or to the dorsolateral part of the "lateral portion of tergum IX" in *N. brevicollis* ["LT.IX" in "Abb. 20", p. 172] of Bils) are heavily sclerotized and asetose in females of all taxa. They are narrow, triangular wedges positioned between the proctiger and the valvifers and narrowly (Fig. 307) to broadly (Fig. 308) continuous (fused) with the latter basally. Interspecific variation in thickness of the connection is evident and useful in relating taxa.

Valvifers

Interspecific differences are evident in several characters of the valvifers ("lateral portion of tergum IX" [possibly fused with the gonangulum] of Bils) among Nearctic *Nebria* (Figs. 307 - 311). Each valvifer is fused with the paraproct dorsobasally and articulates with the coxostylus mediobasally. Overall valvifer shape is similar in females of all taxa; but differences in the shapes and continuity of its sclerotized and membranous areas are apparent. In females of a majority of taxa, the sclerotized area is greatly reduced and confined to a narrow basal strip, expanded only laterally in association with the base of the apodeme (Fig. 309). In females of the remaining taxa,

an additional sclerotized area, separated from the basal strip by a membranous region, is located apicomedially (Fig. 308). It is weakly sclerotized and bears a few short, scattered setae in members of most of these taxa (Fig. 307). In females of *N. virescens*, the area is more heavily sclerotized, with the setae longer and more abundant (Fig. 308). All females of *N. lyelli* and some members of a few other taxa have the medial area weakly sclerotized and asetose (Fig. 310). The basal apodeme is broad and moderately long (Fig. 308) in most females of most species, but short (Fig. 311) in all females of *N. gregaria* Fischer v. Waldheim and *N. arkansana oowah* n. ssp. and some females of a few other taxa. It is positioned laterally in all nebriines.

Tenth sternum

The tenth sternum is represented in nebriines by a pair of small, narrow, pointed lobes (the "rami" or "genital appendages of segment VIII" of Bils) positioned medial to the coxostyli and ventral to the gonopore (Fig. 312). In females of most Nearctic *Nebria*, the lobes are fused to the basimedial angles of the coxostyli (Fig. 312); but in females of a few taxa, they are basally separate from the coxostyli (Fig. 313). I have examined the medial structure described by Edwards (1951) as the "tenth sternite" in *Amphizoa* specimens (Fig. 314) and find its position and articulation quite similar to that of the lobes described above in nebriines. I suggest that these parts are homologous, but cannot extend the suggested homology to particular structures in other groups or in the "generalized insect".

Coxostyli

In all nebriine females sampled, the gonocoxite ("cranial portion of the gonocoxite" of Bils) and the gonostylus ("caudal portion of the gonocoxite" of Bils) are fused to form the coxostylus ("gonocoxite" or "genital appendage of segment IX" of Bils) (Figs. 315 - 321). Fusion is, however, incomplete and restricted to the medial and ventromedial surfaces (Fig. 315). All members of N. darlingtoni n. sp. and N. mannerheimii have the medial face of each coxostylus deeply notched (from the dorsal margin) (Fig. 316) in the area of fusion, thus reducing the apparent extent of connection between the stylus and coxite significantly.

The stylar region of the coxostylus is unilobate, unsegmented, with no secondary or attached lobes or "teeth" (as are seen among cicindelines). In ventral aspect, it is broad basally, markedly arcuate and apically pointed and directed laterad (Fig. 315) in N. virescens females. It is narrower basally, less arcuate and apically pointed and more posterior in direction in females of all other Nearctic taxa (Fig. 316). In lateral aspect, the stylus is slightly to moderately excavate (concave) dorsolaterally and deflected ventrally (Fig. 316) in females of all species except N. virescens, in females of which it is straight (Fig. 315). Interspecific differences in length of the stylus are slight, with stylar length moderate (Fig. 316) in members of most species, longer (Fig. 317) or shorter (Fig. 315) in females of a few. A single, oval subapical pore is present on the ventromedial face (Fig. 315) and bears two long setae (tightly pressed together in most individuals and, therefore, apparent as a single seta).

Associated with the dorsomedial margin of the stylus in all Nearctic females is a row of setae. In females of N. virescens (Fig. 315), the row is composed of three or four medium-length, very stout setae and is positioned diagonally across the medial portion of the dorsal surface (directed basilaterally from the medial margin). In females of all other taxa, the setae are medium-length but slender, and, except in females of N. gebleri Dejean (Fig. 318), the row is positioned along the dorsomedial margin itself (Fig. 317). Both inter- and intraspecific variation in the number of these setae are evident.

The coxite region of the coxostylus is similar in general shape among females of all Nearctic species, with only slight interspecific differences in relative length evident. The dorsal surface of the coxite is open to accommodate muscles inserted internally. The lateral surface (Fig. 316) is membranous apically (basal to the stylus). In ventral aspect, the lateral membranous region is extended medially to a diagonal line (directed apicomedially from the lateral margin to the fused base of the stylus). A row of setae is associated with this line, positioned on the membrane (Fig. 319) on the margin of the sclerotized area (Fig. 316), or in some combination of both positions. In N. virescens Horn females (Fig. 315), the row is composed of five or six long, very stout setae positioned on the margin of the medial sclerotized area. In females of all other taxa, the setae are shorter, more slender, and varied in their position relative to the diagonal margin (Figs. 316 - 320).

The middle portion of the medial surface of the coxostylus bears numerous short, scattered setae in members of most species (Fig. 316), but is more sparsely (Fig. 321) or densely (Fig. 315) setose in

members of a few. Setae are entirely absent (Fig. 320) from females of some species (e.g. N. nivalis) or present, but very short and restricted to the apical half of the medial surface (Fig. 319), in those of a few other species. Dorsal, lateral and ventral surfaces of the coxostylus are asetose, except in N. virescens females, which have the setal field of the medial surface continued on the medial edge of the ventral surface (Fig. 315).

Bursa copulatrix

The general form of the bursa copulatrix in females of the trifaria group (sensu Ball and Erwin, 1972) of Nebria was illustrated by these authors with more detailed drawings of certain sclerites found on the bursa. This pioneer effort in the study of internal female genitalic structure in nebriines prompted me to include a more comprehensive survey of these structures in my own project as both an aid in interpreting their findings and a potential source of additional characters of use in studying members of the Nearctic fauna. The structures examined differed in numerous characters as discussed below.

I found few if any differences in shape or other characters among conspecifc specimens that could be attributed to manner of preservation of the specimens (e.g. as dried specimens, or specimens killed and/or preserved in 70% ethyl alcohol, Bouin's solution, or Weaver's Fixative). I conclude that preservation technique is not of prime importance for the study of bursa and associated structures (see comments of Erwin and Ball, 1972:78). However, interpretation of shape and orientation of these structures is extremely difficult if a mixture of specimens with genitalia in various states of extension or retraction is studied. I

obtained best results (i.e. simplest comparisons) by restricting my dissections of internal structures to specimens in which the genitalia were fully retracted. An additional problem was encountered as a result of heating the specimens during relaxation and/or treatment with potassium hydroxide (see methods, section 2.22 above). If specimens are heated too rapidly, the genitalia of some are explosively everted. In such instances, the bursa may become completely everted (turned inside out), presenting a confounding arrangement of parts and completely confusing any attempts at their proper orientation. Ali's (1967) description of the internal structures of the female genitalia in Notiophilus (? sp.) fits the arrangement of parts in such an 'exploded' specimen perfectly; and, in fact, I suggest that the peculiar arrangement of parts he described is an artifact of preparation [because all Notiophilus specimens I studied were very similar in structure to nebriines and not as described by Ali]. Specimens taken directly from fluid preservation (especially alcohols) must be slowly heated.

For convenience (and, in part, structurally) the bursa copulatrix (Figs. 322 - 344) is divided into a posterior 'vestibular chamber' and an anterior (or dorsal) 'spermathecal chamber' (refer to Figs. 322 - 323 for an illustration of terms used in relation to bursal and associated structures). The 'vestibulat chamber' is open posteriorly through the gonopore, receives the common oviduct ventrally and is continuous with the 'spermathecal chamber' anterodorsally but partitioned from the latter at a dorsal flexure of the bursa (see below). The 'spermathecal chamber' is dorsal and, in females of most

taxa, anterior to the 'vestibular chamber' and bears the opening of the spermathecal duct (see below). Interspecific differences are evident in the main longitudinal axis of the bursa (i.e. a line drawn from the gonopore to the apex of the 'spermathecal chamber' along the midline) in lateral aspect. In _N. virescens_ females, the axis is weakly deflected dorsally (Fig. 324). In females of other taxa, the axis is more strongly deflected dorsally (Figs. 325-326), recurved posterodorsally (Fig. 327), or loosely (Fig. 335) or tightly (Fig. 329) sigmoidal. Interspecific differences in shape of the 'spermathecal chamber' tend to obscure axis direction in some instances.

The confluence of the common oviduct with the 'vestibular chamber' is ventral and near the gonopore (Fig. 323) in all Nearctic females. The chamber is, therefore, very short ventrally but longer dorsally and laterally. In dorsal aspect, it is very broad, symmetrical and bell-shaped. The anterolateral angles of the chamber are weakly (Fig. 327) to markedly (Fig. 330) flared or recurved posteriorly (Fig. 336) among females of different taxa.

Shape of the 'spermathecal chamber' is quite complex and difficult to describe, due especially to variation in its orientation accompanying differences in direction of the longitudinal bursal axis. In dorsal aspect, it is distinctly narrower than the 'vestibular chamber' (Fig. 334) in females of all species except _N. virescens_ (Fig. 324) and _N. paradisi_ (Fig. 340), in females of which it is very slightly narrower than or equal in width to (respectively) the 'vestibular chamber'. Again in dorsal aspect (ventral aspect if the bursal axis is recurved posteriorly; apical aspect if the axis is deflected directly dorsad), the chamber is symmetrical (Fig. 328) in females of most taxa,

but apically deflected right (Fig. 327) or left (Fig. 326) in females of a few; and it is extremely varied in shape -- broadly lobate (Figs. 324a,324b), spatulate (Fig. 335), quadrate (Figs. 326 - 327), longitudinally (Fig. 341) or transversely (Fig. 329) ovoid, or some variant of one of these forms. In lateral aspect, the chamber is varied in length, from short (Fig. 327) to long (Fig. 324), but moderate in length (Fig. 334) in females of most taxa. Shape in lateral aspect is also varied among females of different taxa -- thin, longitudinally lobate (Fig. 324), thin, fusiform (Fig. 335), thick, globose (Fig. 328) or thick and apically narrowed and straight (Fig. 338) or anteriorly (Fig. 330) or posteriorly (Fig. 325) recurved. Slight intraspecific variation in different aspects of shape of the chamber is evident in most species, but considerably less than interspecific variation in the same characters.

There appear to be no dorsal or ventral chambers of the bursa separate from its two-chambered main axis among females of Nearctic taxa. The 'spermathecal chamber' itself, however, has one or more accessory lobes in members of certain taxa. Nebria desolata Kavanaugh females (Fig. 342) have a pair of thick, elongate accessory lobes on the dorsal surface of the chamber. Females of N. kincaidi and related taxa (but not N. carri n. sp.) have a thin, boat-like lobe (Fig. 335) (varied in length among members of these taxa) on the posterior surface of the chamber, which partially sheaths the base of the spermathecal duct and its insertion. Nebria paradisi Darlington is unique among Nearctic taxa in that its females have a small accessory lobe on the anteroventral surface of the chamber (Fig. 340). As noted below, the

basal portion of the spermathecal duct is (apparently) thickened abruptly (Figs. 327, 333) in females of a few taxa. In such instances, the swollen duct mimics an accessory lobe on the chamber (which it may actually be).

The shapes of certain parts of the bursa are rigidly maintained by the presence of sclerites (or at least more heavily sclerotized areas) or a reinforcement rod in females of almost all Nebria taxa. Sclerites are restricted to three bursal regions among members of Nearctic taxa. In all N. paradisi Darlington females examined, a pair of broad, flat, weakly sclerotized paramedial plates were located in the dorsal wall of the 'vestibular chamber' (Fig. 340). Neither these nor any other sclerite are located in this chamber in females of other taxa. A second location for bursal sclerites is in the posterior or dorsal wall (depending on bursal axis orientation) of the 'spermathecal chamber'. If present, a sclerite is, in females of most taxa, closely associated with the insertion of the spermathecal duct (Fig. 338) (remotely associated [Fig. 342] in members of a few taxa). Females of many taxa (including all those in which members have the duct inserted ventral) have no sclerite in this wall of the chamber (Fig. 325). In females of almost all Nearctic taxa, a distinct, opaque reinforcement rod is present (Fig. 323) in the ventral wall of the 'spermathecal chamber', extended posteriorly into the 'vestibular chamber' to the confluence of the latter with the common oviduct, then reversed anteriorly in the dorsal wall of the oviduct (see below). In females of N. obliqua and related species, the rod is weakly developed and restricted to the 'vestibular chamber' of the bursa (Fig. 343). It is further extended

anterodorsally (Fig. 325) in the ventral wall of the 'spermathecal chamber' in females of some taxa (especially those in which members have the spermathecal duct inserted ventrally) and/or apically broadened and plate-like (Figs. 326, 344). It is non-sclerotized (possibly composed of resilin) in all nebriines examined. The third location for bursal sclerites, however, is in association with the apex of this rod (Figs. 326, 344) (i.e. in the ventral, or anterior wall of the 'spermathecal chamber'). If present, the sclerite is also associated with the insertion of the spermathecal duct (Fig. 344), except as present in females of _N. pallipes_, _N. gebleri rathvoni_ LeConte, or _N. gebleri strawberriensis_ n. ssp., which have the duct insertion on the posterior wall of the chamber.

Interspecific and interpopulational differences in the shape, size and position of various bursal sclerites are often quite striking. Descriptions of these sclerites are presented below, with descriptions of the taxa (section 3.43). Both similarities within and differences between species groups are also evident in characters of the sclerites, and they are, therefore, quite useful in testing hypotheses on relationships suggested by analyses based on other characters. Interpopulational variation in size and shape of the sclerites was seen in several taxa; but as noted by Erwin and Ball (1972) in their study, this variation is slight compared with interpopulational differences.

Spermatheca and associated structures

Due principally to the pioneer work of L. Schuler (see for example Schuler, 1960, 1962 or 1965), the spermathecae and associated structures in carabids are now frequently examined in systematic

studies. Differences I observed in these structures among females of Nearctic Nebria are less striking than some reported by Schuler among females of other groups, but quite useful nonetheless.

The spermatheca is very weakly sclerotized in all Nearctic females. In females of most species, it is short, narrow, arcuate and lanceolate (Fig. 345); but in those of a few other species it is less arcuate (Fig. 346) or elongate, convoluted and apically (Fig. 347) or subapically (Fig. 348) swollen.

As noted by Ali (1967), a spermathecal gland, present in Notiophilus females (Fig. 349), is lacking from Nebria females.

The spermathecal duct is also very weakly sclerotized in all nebriines examined. Interspecific differences are evident in length, shape and diameter of the duct. Among females of different taxa, range in duct length is from short (Fig. 336) to long (Fig. 351). In shape, the duct is loosely (Fig. 346) or tightly (Fig. 351) and unevenly convoluted or evenly sinusoidal (Fig. 350). Differences in diameter of the duct are conspicuous, ranging from very narrow (Fig. 345) in females of most taxa to moderately (Fig. 346) or very (Fig. 352) thick in those of a few. As discussed above, females of some taxa have either the basal portion of the duct abruptly thickened (Figs. 347, 352) or the duct itself inserted at the apex of an accessory lobe of the 'spermathecal chamber'. Interpretations of relationship between the bursa and the duct made for individual taxa are discussed in descriptions of the taxa (section 3.43).

Interspecific variation in the point of insertion of the spermathecal duct on the bursa has been noted above. Insertion is on

the midline (Fig. 324) in members of most taxa, but displaced slightly to the right in N. frigida Sahlberg females (Fig. 327) and to the left in females of a few related taxa (Fig. 326), in association with similar asymmetry in the apex of the 'spermathecal chamber'. The duct inserts on the posterior (or dorsal) surface of the chamber (Figs. 340, 331) in females of most species, on the anterior (or ventral) surface in those of a few species. Interspecific differences in the precise point of insertion on either face are also evident and noted in the descriptions of taxa.

Common oviduct

I did not study form and structure of the common oviduct in Nearctic Nebria; but I should note that, in all females examined in which a remnant of the oviduct was present, the ventral reinforcement rod described above in the bursa extended anteriorly in the common oviduct as well (Fig. 354). In at least some females, the rod extends for a short distance in the dorsal wall, then loops transversely and/or ventrally (Fig. 353) and imparts a rigid and specific shape to the oviduct at that point.

3.22 Chorology

Study of geographical distributions is of prime importance in systematics for providing an accessible and unique set of characters of use in studying taxa. Knowledge of present distributions of taxa can help to elucidate their past distributions and evolutionary histories as well as phylogenetic relationships among them (Hennig, 1966). In addition, analysis of present distributions of taxa in single groups provides derivative data of use in recognition and study of general (synoptic) biogeographical patterns. Because geographical data are essentially independent of data acquired through morphology and other studies, distributional patterns can be used in tests for consistency among relationships inferred from the analyses of these other data (Mayr, 1969) (see section 4.3 below for discussion of compatibility of the proposed phylogeny with zoogeographic reconstructions).

Distributional data are of particular relevance to application of the species and subspecies concepts outlined above (section 2.29). Knowledge of geographical relations (i.e. sympatry, parapatry or allopatry) of different populations of the same or different species-group taxa is often crucial in determining their probable status.

My original intent was to present a separate, detailed discussion of Nearctic Nebria distribution equivalent to the preceding treatment of form and structure. However, because data on the distributions of individual taxa are presented with the taxon descriptions and comparisons of distributions and analyses of distributional patterns are treated with other data in section 4.22 on contemporary zoogeography, there is no need to repeat details here. This section is,

therefore, restricted to a brief discussion of the characters used and the kinds of data acquired. My purpose is to stress the need to consider distributional characters in the same perspective as structural or any other characters. Characters used apply either to single localities where members of a taxon have been found or to the known geographical range of a taxon; and these classes of characters are discussed separately below.

3.221 Characters of single localities

Knowledge of distributions of taxa is dependent on accumulation of observations on their occurrence in particular places, localities; and these are characterized in a number of ways. Each is identified in this study according to political units (i.e. country; state, province or territory; and county or district) and place name. Because the boundaries of political units are subject to change and their permanence is often questionable, and because place names may change with time or become inappropriate as human activity alters the surface features of a region, it has been argued that latitudinal and longitudinal geographical coordinates are preferable locality designations. However, the relocation of these localities, by subsequent workers interested in collecting or observing individuals of a particular taxon, from coordinate data alone requires detailed maps not readily available or equipment not in everyday use. In contrast, place names are normally recognized through the use of readily available maps or from a variety of local information sources. The large amount of locality data presented here precludes presentation of

both place names and coordinates for each. A list of localities is provided (see Appendix B) for each of the Nearctic taxa, and dot maps (Figs. 380 - 411) illustrate the distributions of these known localities.

As noted above, most Nebria members occupy montane, riparian habitats. In this study, it was therefore useful to characterize each locality (if appropriate) in terms of its relationship to a mountain range or system and/or drainage system. These data for each taxon are summarized under the geographical distribution section of its description (section 3.43) and in Tables 2 (see also Table 1) and 4 (see also Table 3), respectively.

Presence or absence of members of other Nebria taxa was recorded (when possible) for each locality of a taxon. These data on microsympatry (or indirect evidence for microallopatry or microparapatry) are of use, as noted above, in application of species and subspecies concepts as well as in considerations of possible interactions (e.g. competitive exclusion) among taxa. Data are summarized in Table 5.

3.222 Known ranges of taxa

Characters used in study of the ranges of Nearctic Nebria taxa include their relationship to political, physiographic and faunal regions and their size, continuity and geographical relations with the ranges of other taxa. An attempt was made to relate the geographical distributions of all taxa (Figs. 380 - 411) to major faunal regions, physiographic features and major political units and record these data.

Table 1. Mountain systems and ranges of North America[1, 2]

1. Pacific Coast Range system
   - A. Alaskan Coast Ranges
     - a. Aleutian Range
     - b. Alaskan Range
     - c. Chugach Mountains
     - d. Wrangell and St. Elias Mountains
   - B. North Coastal Mountains
   - C. Coastal Mountains of Puget Sound area
     - a. Vancouver Island Mountains
     - b. Olympic Mountains
   - D. Middle Coast Ranges
     - a. Coast Range of Oregon
     - b. Siskiyou Mountains
     - c. Klamath Mountains system
     - d. Coast Range of northern California
   - E. South Coast Ranges
     - a. Santa Cruz Diablo, and Santa Lucia Ranges
     - b. San Gabriel and San Bernardino Ranges
2. Cascade-Sierra Nevada Mountain system
   - A. Cascade Range
     - a. Cascade Range north of Columbia River
     - b. Cascade Range south of Columbia River
   - B. Sierra Nevada
     - a. Sierra Nevada north of Mammoth Lakes area
     - b. Sierra Nevada south of Mammoth Lakes area

Table 1. (continued)

3. Plateau and Basin and Range Provinces

   A. Yukon Plateau

   B. Northern interior ranges

      a. Cassiar, Skeena and Omineca Mountains

   C. Fraser Plateau

      a. Cariboo and Columbia Mountains

   D. Columbia Plateau

      a. Clearwater Mountains

      b. Salmon River Mountain system

      c. Seven Devils Mountains

      d. Wallowa Mountains

      e. Blue Mountains

   E. Ranges of Basin and Range Province[3]

      a. Warner Mountains

      b. Washoe Mountains

      c. Independence Mountains

      d. Jarbridge Mountains

      e. Ruby Mountains

      f. Toiyabe Mountains

      g. Stansbury Mountains

      h. Pavant Mountains, Tushar Range, and Midget Crest

      i. Parowan and Cedar Mountains

      j. Pine Valley Mountains

   F. Colorado Plateau

      a. Markagunt Plateau

Table 1. (continued)

b. Sevier Plateau

c. Paunsaugunt Plateau

d. Aquarius Plateau

e. Henry Mountains

f. La Sal Mountains

g. Abajo Mountains

h. Chuska Mountains

4. Rocky Mountain System

A. Alaska-Yukon Rocky Mountains

a. Brooks Range

b. Richardson, Ogilvie, Mackenzie, Selwyn, and Pelly Mountains

B. Northern Rocky Mountains

a. Rocky Mountains north of Peace River

b. Front Ranges of Alberta and Montana (includes Cypress Hills, Big Snowy Mountains, etc.)

c. Selkirk Mountains

d. Bitterroot Mountains

e. Absaroka Plateau

f. Bighorn Mountains

C. Central Rocky Mountains

a. Black Hills

b. Teton Range

c. Gros Ventre Range

d. Wind River Range

Table 1. (continued)

e. Wyoming, Salt River, Snake River, and Bear River Ranges

f. Wasatch Range

g. Uinta Mountains

D. Southern Rocky Mountains

a. Laramie Mountains

b. Medicine Bow Mountains

c. Park Range

d. Front Range of Colorado

e. Sawatch Range and Elk Mountains

f. Gore, Mosquito, and Tenmile Ranges

g. White River Mountains

h. Grand Mesa

i. Uncompahgre Plateau

j. Sangre de Cristo Range and Wet Mountains

k. Sacramento Mountains

l. San Juan Mountains

m. Jemez Mountains

5. Ozark System

a. Ozark Plateau

b. Boston Mountains

c. Ouchita Mountains

6. Appalachian Mountain System

A. Northern Ranges

a. Notre Dame Mountains

b. Longfellow Mountains

Table 1. (continued)

c. White Mountains

d. Green Mountains

e. Adirondack Mountains

B. Blue Ridge Mountains

a. Blue Ridge north of French Broad River

b. Blue Ridge south of French Broad River

C. Appalachia Ridges and Plateau

a. Catskill Mountains

b. Allegheny Plateau

c. Cumberland Plateau

---

[1] The classification of mountain systems and ranges used here is my own, based in part on those of Fenneman (1931 and 1938) and Map Information Office, U. S. Federal Board of Surveys and Maps (1929) (see also Clark and Stearn, 1968). All units are grouped for convenience in discussion of *Nebria* distribution and, therefore, are not necessarily placed with other units having similar geologic history. Refer to Fig. 428 for illustration of the above classification. The alpha-numeric code presented here is used in Table 2 on the distributions of Nearctic *Nebria* taxa.

[2] Only mountain systems and/or ranges known to be inhabited by *Nebria* populations have been included. One exception, however, is the Ozark system, from which *Nebria* are not yet known. I list the Ozark system here to emphasize that point.

[3] Sampling for *Nebria* populations in the Basin and Range Province is

yet very incomplete; and such populations undoubtedly inhabit ranges not listed here.

Table 2. Distribution of Nearctic <u>Nebria</u> taxa in relation to mountain systems and ranges.[1]

	Mountain system (1)													(2)				(3)																	
	A Alaskan Coast				B North Coast	C Puget Coast		D Middle Coast				E South Coast		A Cascade		B Sierra Nevada		A Yukon Pl.	B No. Interior	C Fraser Pl.	D Columbia Pl.					E Basin & Range									
Name of Taxon	a	b	c	d		a	b	a	b	c	d	a	b	a	b	a	b		a	a	a	b	c	d	e	a	b	c	d	e	f	g	h	i	j
virescens						X	X							X	X	X	X				X				X	X									
paradisi														x	x																				
gouleti						X															X	X		X	X										
hudsonica				X														X	X	X															
l. lacustris																																			
l. bellorum																																			

Table 2. (continued)

	Mountain system																																			
	(3)								(4)																											
	F Colorado Pl.								A Al.-Yu. Rockies		B No. Rockies						C Cent. Rockies							D So. Rockies												
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
virescens																																				
paradisi																																				
gouleti																																				
hudsonica											X	X	X	X	X		X	X	X	X	X	X			X		X	X	X	X						
l. lacustris																																				
l. gaspesiana																																				

Table 2. (continued)

Name of Taxon	Mountain system (5) Ozark Plateau			(6) A North. Ranges					B Blue Ridge		C Ridges and Plateau		
	a	b	c	a	b	c	d	e	a	b	a	b	c
virescens													
paradisi													
gouleti													
hudsonica													
l. lacustris						X	X	X	X		X	X	X
l. bellorum										X			

Table 2. (continued)

	(1)													(2)				(3)																	
	A				B	C		D				E		A		B		A	B	C	D					E									
Name of taxon	a	b	c	d		a	b	a	b	c	d	a	b	a	b	a	b		a	a	a	b	c	d	e	a	b	c	d	e	f	g	h	i	j
n. nivalis	X	X	X	X														X	X	X															
n. gaspesiana																																			
c. crassicornis							X							X																					
c. intermedia					X													X	X	X				X	X										
gyllenhali castanipes														X				X	X	X	X	X		X	X					X					
g. lassenensis															X	X																			
g. lindrothi																																			
frigida	X	X	X	X														X	X																
lyelli																X																			
a. acuta			X	X	X									X	X	X																			
a. quileute							X																												

Table 2. (continued)

	(3)								(4)																											
	F								A		B						C							D												
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
n. nivalis									X	X																										
n. gaspesiana																																				
c. crassicornis																																				
c. intermedia	X										X	X	X	X	X			X	X	X	X	X	X													
gyllenhali castanipes											X	X	X	X	X	X	X	X	X	X				X												
g. lassenensis																																				
g. lindrothi						X																			X	X	X	X	X	X	X	X	X		X	X
frigida									X	X	X																									
lyelli																																				
a. acuta																																				
a. quileute																																				

Table 2. (continued)

Name of taxon	(5)			(6)									
				A					B		C		
	a	b	c	a	b	c	d	e	a	b	a	b	c
n. nivalis													
n. gaspesiana				X	X								
c. crassicornis													
c. intermedia													
gyllenhali castanipes					X	X		X					
g. lassenensis													
g. lindrothi													
frigida													
lyelli													
a. acuta													
a. quileute													

Table 2. (continued)

Name of taxon	(1)													(2)				(3)																	
	A				B	C		D				E		A		B		A	B	C	D					E									
	a	b	c	d		a	b	a	b	c	d	a	b	a	b	a	b		a	a	a	b	c	d	e	a	b	c	d	e	f	g	h	i	j
s. sahlbergii	X		X	X	X	X	X	X						X	X			X	X	X					X										
s. modoc																										X									
s. triad										X																									
gregaria	X																																		
charlottae					X																														
a. arkansana																																			
a. edwardsi																		X		X		X		X	X										
a. oowah																																			
a. uinta																																			
f. fragilis																																			
f. teewinot																																			

Table 2. (continued)

	(3)								(4)																											
	F								A		B						C							D												
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
s. sahlbergii											X	X	X																							
s. modoc																																				
s. triad																																				
gregaria																																				
charlottae																																				
a. arkansana							X																	X	X	X	X	X	X		X	X			X	X
a. edwardsi											X	X	X	X	X	X																				
a. oowah						X																														
a. uinta																					X	X														
f. fragilis																					X															
f. teewinot																	X	X	X	X																

Table 2. (continued)

Name of taxon	(5)			(6)									
				A					B		C		
	a	b	c	a	b	c	d	e	a	b	a	b	c
s. sahlbergii													
s. modoc													
s. triad													
gregaria													
charlottae													
a. arkansana													
a. edwardsi													
a. oowah													
a. uinta													
f. fragilis													
f. teewinot													

Table 2. (continued)

	(1)													(2)				(3)																	
	A				B	C		D				E		A		B		A	B	C	D					E									
Name of taxon	a	b	c	d		a	b	a	b	c	d	a	b	a	b	a	b		a	a	a	b	c	d	e	a	b	c	d	e	f	g	h	i	j
z. zioni																																	X	X	
z. oasis																																			X
suturalis																																			
obliqua			X	X	X									X		X		X	X	X	X	X		X	X	X		X	X	X	X		X	X	
appalachia																																			
pallipes																																			
darlingtoni																X																			
mannerheimii			X	X	X	X	X	X						X	X				X	X					X										
desolata																																			
navajo																																			
eschscholtzii							X	X	X	X	X	X	X	X	X	X	X				X				X		X								

Table 2. (continued)

	(3)								(4)																											
	F								A		B						C							D												
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
z. zioni	X	X	X																																	
z. oasis																																				
suturalis												X						X									X		X							
obliqua	X	X	X					X			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X		X	X
appalachia																																				
pallipes																																				
darlingtoni																																				
mannerheimii													X																							
desolata				X	X																															
navajo																																				
eschscholtzii																																				

Table 2. (continued)

Name of taxon	(5) a	(5) b	(5) c	(6) A a	(6) A b	(6) A c	(6) A d	(6) A e	(6) B a	(6) B b	(6) C a	(6) C b	(6) C c
z. zioni													
z. oasis													
suturalis						X	X	X					
obliqua													
appalachia									X	X			
pallipes					X	X	X	X	X	X	X	X	X
darlingtoni													
mannerheimii													
desolata													
navajo													
eschscholtzii													

Table 2. (continued)

	(1)													(2)				(3)																	
	A				B	C		D				E		A		B		A	B	C	D					E									
Name of taxon	a	b	c	d		a	b	a	b	c	d	a	b	a	b	a	b		a	a	a	b	c	d	e	a	b	c	d	e	f	g	h	i	j
diversa																																			
g. gebleri					X														X	X	X	X	X	X	X										
g. cascadensis					X	X								X	X																				
g. rathvoni																X	X																		
g. siskiyouensis									X	X																									
g. strawberriensis																									X										
carri																						X	X												
k. kincaidi					X	X	X							X																					
k. balli														X	X																				
s. spatulata																	X																		
s. sierrae																X	X																		

Table 2. (continued)

	(3)								(4)																											
	F								A		B						C							D												
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
diversa																																				
g. gebleri											X	X	X	X																						
g. cascadensis																																				
g. rathvoni																																				
g. siskiyouensis																																				
g. strawberriensis																																				
carri																																				
k. kincaidi																																				
k. balli																																				
s. spatulata																																				
s. sierrae																																				

Table 2. (continued)

	(5)			(6)								
				A					B		C	
Name of taxon	a	b	c	a	b	c	d	e	a	b	a	b	c
diversa													
g. gebleri													
g. cascadensis													
g. rathvoni													
g. siskiyouensis													
g. strawberriensis													
carri													
k. kincaidi													
k. balli													
s. spatulata													
s. sierrae													

Table 2. (continued)

	(1)													(2)				(3)																	
	A				B	C		D				E		A		B		A	B	C	D					E									
Name of taxon	a	b	c	d		a	b	a	b	c	d	a	b	a	b	a	b	a	a		a	b	c	d	e	a	b	c	d	e	f	g	h	i	j
ovipennis																X	X										X								
m.meanyi					X									X	X																				
m. lamarckensis																	X																		
m. sylvatica						X	X																												
metallica	X		X		X	X	X							X																					
i. ingens																	X																		
i. riversi																X																			
v. vandykei							X							X																					
v. wyeast															X																				
piperi					X		X							X	X																				
s. schwarzi																																			

Table 2. (continued)

	(3)								(4)																											
	F								A		B						C							D												
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
ovipennis																																				
m. meanyi																																				
m. lamarckensis																																				
m. sylvatica																																				
metallica											X	X	X	X																						
i. ingens																																				
i. riversi																																				
v. vandykei																																				
v. wyeast																																				
piperi											X																									
s. schwarzi												X																								

Table 2. (continued)

	(5)			(6)								
				A					B		C	
Name of taxon	a	b	c	a	b	c	d	e	a	b	a	b	c
ovipennis													
m. meanyi													
m. lamarckensis													
m. sylvatica													
metallica													
i. ingens													
i. riversi													
v. vandykei													
v. wyeast													
piperi													
s. schwarzi													

Table 2. (continued)

	(1)													(2)				(3)																	
	A				B	C		D				E		A		B		A	B	C	D					E									
Name of taxon	a	b	c	d		a	b	a	b	c	d	a	b	a	b	a	b	a	a		a	b	c	d	e	a	b	c	d	e	f	g	h	i	j
s. beverlianna																																			
purpurata																																			
t. trifaria																													X	X	X				
t. catenata																																			
t. utahensis																																			
coloradensis																																			
piute																																X			

Table 2. (continued)

	(3)								(4)																											
	F								A		B						C							D												
Name of taxon	a	b	c	d	e	f	g	h	a	b	a	b	c	d	e	f	a	b	c	d	e	f	g	a	b	c	d	e	f	g	h	i	j	k	l	m
s. beverlianna																			X																	
purpurata																											X	X	X				X		X	X
t. trifaria	X	X	X	X											X			X	X	X	X	X	X	X	X	X	X									
t. catenata						X	X																									X		X	X	
t. utahensis					X																															
coloradensis																												X	X	X	X					
piute																																				

Table 2. (continued)

	(5)			(6)								
				A					B		C	
Name of taxon	a	b	c	a	b	c	d	e	a	b	a	b	c
s. beverlianna												
purpurata												
t. trifaria												
t. catenata												
t. utahensis												
coloradensis												
piute												

1 Refer to Table 1 for explanation of code for mountain systems and ranges. An "X" in any column denotes occurrence of a taxon in the mountain range or system represented.

Table 3. Principal drainage systems of North America[1]

1. California Central Valley drainage
    - A. Sacramento River system
    - B. San Joaquin River system
2. Mid-Pacific coastal drainage
    - A. Klamath River system
    - B. Rogue River system
    - C. Umpqua River system
3. Columbia River drainage
    - A. Willamette River system
    - B. Deschutes River system
    - C. John Day River system
    - D. Snake River system
    - E. Columbia River system
    - F. Okanagan River system
    - G. Yakima River system
4. Fraser River drainage
    - A. Fraser River system
    - B. Thompson River system
5. North-Pacific coastal drainage
    - A. Puget Sound local drainage
    - B. Skeena River system
    - C. Stikine River system
    - D. Copper River system
    - E. Susitna River system

Table 3. (continued)

6. Yukon River drainage
   A. lower Yukon River
   B. Koyukuk River system
   C. Tanana River system
   D. Porcupine River system
   E. upper Yukon River system
7. Mackenzie River drainage
   A. lower Mackenzie River
   B. Liard River system
   C. Hay River system
   D. Peace River system
   E. Athabasca River system
8. Nelson River-Lake Winnipeg drainage
   A. North Saskatchewan River system
   B. South Saskatchewan River system
   C. Assiniboine River-Red River systems
9. Great Basin internal drainage
10. Colorado River drainage
    A. San Juan River system
    B. upper Colorado River system
    C. Green River system
    D. lower Colorado River system
    E. Virgin River system

Table 3. (continued)

11. Rio Grande River drainage
    A. Rio Grande River system
    B. Pecos River system
12. Mississippi River drainage, I. Arkansas Unit
    A. Arkansas River system
13. Mississippi River drainage, II. Missouri Unit
    A. South Platte River system
    B. North Platte River system
    C. Yellowstone River system
    D. upper Missouri River system
    E. Cheyenne River system
14. Mississippi River drainage, III. Mississippi Unit
    A. upper Mississippi River system
15. Mississippi River drainage, IV. Ohio Unit
    A. Ohio River system
16. Atlantic coastal drainage
17. St. Lawrence River-Great Lakes drainage
18. East-Arctic drainage
19. Mid-Arctic drainage
    A. Churchill River system
    B. Anderson River system

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[1] Refer to Fig. 429 for illustration of the above drainage classification. The alpha-numeric code presented here is used in Table 4 on the distributions of Nearctic _Nebria_ taxa.

Table 4. Distribution of Nearctic Nebria taxa in relation to drainage systems.[1]

Drainage system

Name of taxon	1 California		2 Mid-Pacific			3 Columbia							4 Fraser		5 No.-Pacific					6 Yukon					7 Mackenzie					8 Nelson			9 Great Basin
	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	
virescens	X	X		X	X	X			X		X	X	X		X																		
paradisi							X					X			X																		
gouleti									X	X																							
hudsonica									X	X		X	X	X		X	X							X		X		X	X	X	X		X
l. lacustris																																X	
l. bellorum																																	
n. nivalis																		X	X	X	X	X	X	X	X			X					
n. gaspesiana																																	

Table 4. (continued)

	Drainage system																		
	10 Colorado					11 Rio Grande		12 Arkansas U.	13 Missouri U.					14 upper Miss.	15 Ohio Unit	16 Atlantic	17 St. Lawrence	18 East-Arctic	19 Mid-Arctic	
Name of taxon	A	B	C	D	E	A	B	A	A	B	C	D	E	A	A				A	B
virescens																				
paradisi																				
gouleti																				
hudsonica		X	X					X	X	X	X	X								
l. lacustris														X	X	X	X			
l. bellorum																X	X			
n. nivalis																		X	X	X
n. gaspesiana																	X	X		

Table 4. (continued)

Name of taxon	1		2			3							4		5					6					7					8			9
	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	
c. crassicornis												X	X		X																		
c. intermedia									X	X			X	X												X	X	X	X	X	X		X
gyllenhali castanipes									X	X	X	X	X	X		X	X			X				X	X	X	X	X	X	X	X	X	
g. lassenensis	X						X																										
g. lindrothi																																	
frigida																			X	X		X	X	X		X							
lyelli		X																															
a. acuta	X					X	X					X	X		X	X	X	X	X														
a. quileute															X																		
s. sahlbergii						X	X		X	X	X	X	X	X	X	X	X	X	X					X		X		X	X	X			
s. modoc	X																																
s. triad	X																																
gregaria																																	

Table 4. (continued)

Name of taxon	10					11		12	13					14	15	16	17	18	19	
	A	B	C	D	E	A	B	A	A	B	C	D	E	A	A				A	B
c. crassicornis																				
c. intermedia			X								X	X								
gyllenhali castanipes			X							X	X	X	X			X	X	X		
g. lassenensis																				
g. lindrothi	X	X				X	X	X	X	X										
frigida																				X
lyelli																				
a. acuta																				
a. quileute																				
s. sahlbergii																				
s. modoc																				
s. triad																				
gregaria																				

Table 4. (continued)

	1		2			3							4		5					6					7					8			9
Name of taxon	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	
charlottae																																	
a. arkansana																																	
a. edwardsi									X	X	X															X			X	X	X		X
a. oowah																																	
a. uinta																																	X
f. fragilis																																	X
f. teewinot									X																								
z. zioni																																	X
z. oasis																																	
suturalis									X																				X				
obliqua							X	X	X	X	X	X	X	X		X	X	X						X		X	X	X	X	X	X		X
appalachia																																	

Table 4. (continued)

Name of taxon	10 A	10 B	10 C	10 D	10 E	11 A	11 B	12 A	13 A	13 B	13 C	13 D	13 E	14 A	15 A	16	17	18	19 A	19 B
charlottae																				
a. arkansana	X	X				X	X	X	X	X										
a. edwardsi											X	X								
a. oowah		X																		
a. uinta			X																	
f. fragilis																				
f. teewinot			X																	
z. zioni					X															
z. oasis					X															
suturalis		X							X							X	X	X		
obliqua	X	X	X		X	X	X	X	X	X	X	X	X							
appalachia															X	X				

Table 4. (continued)

	1		2			3							4		5					6					7					8			9
Name of taxon	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	
pallipes																																	
darlingtoni	X																																
mannerheimii						X		X	X	X	X	X	X	X	X	X	X	X															
desolata																																	
navajo																																	
eschscholtzii	X	X	X	X	X	X	X	X	X	X		X			X																		X
diversa																																	
g. gebleri								X	X	X	X		X	X		X	X							X		X		X	X	X	X		
g. cascadensis						X	X				X	X	X	X	X																		
g. rathvoni	X	X																															
g. siskiyouensis			X	X																													
g. strawberriensis								X																									
carri									X																								

Table 4. (continued)

Name of taxon	10 A	10 B	10 C	10 D	10 E	11 A	11 B	12 A	13 A	13 B	13 C	13 D	13 E	14 A	15 A	16	17	18	19 A	19 B
pallipes														X	X	X	X			
darlingtoni																				
mannerheimii																				
desolata				X	X															
navajo				X																
escscholtzii																				
diversa																				
g. gebleri											X	X								
g. cascadensis																				
g. rathvoni																				
g. siskiyouensis																				
g. strawberriensis																				
carri																				

Table 4. (continued)

Name of taxon	1		2			3							4		5					6					7					8			9
	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	
k. kincaidi															X	X	X																
k. balli						X	X					X			X																		
s. spatulata		X																															
s. sierrae		X																															
ovipennis	X	X																															X
m. meanyi	X					X	X					X			X	X	X																
m. lamarckensis																																	X
m. sylvatica															X																		
metallica										X			X		X		X	X	X									X	X				
i. ingens		X																															X
i. riversi		X																															X
v. vandykei												X			X																		
v. wyeast						X	X																										

Table 4. (continued)

	10					11		12	13					14	15	16	17	18	19	
Name of taxon	A	B	C	D	E	A	B	A	A	B	C	D	E	A	A				A	B
k. kincaidi																				
k. balli																				
s. spatulata																				
s. sierrae																				
ovipennis																				
m. meanyi																				
m. lamarckensis																				
m. sylvatica																				
metallica																				
i. ingens																				
i. riversi																				
v. vandykei																				
v. wyeast																				

Table 4. (continued)

Name of taxon	1		2			3							4		5					6					7					8			9
	A	B	A	B	C	A	B	C	D	E	F	G	A	B	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	
piperi						X						X	X	X	X	X	X									X							
s. schwarzi										X																			X	X	X		
s. beverlianna									X																								
purpurata																																	
t. trifaria									X																								X
t. catenata																																	
t. utahensis																																	
coloradensis																																	
piute																																	X

Table 4. (continued)

Name of taxon	10 A	10 B	10 C	10 D	10 E	11 A	11 B	12 A	13 A	13 B	13 C	13 D	13 E	14 A	15 A	16	17	18	19 A	19 B
piperi																				
s. schwarzi																				
s. beverlianna																				
purpurata	X	X				X		X	X											
t. trifaria		X	X		X			X	X	X	X									
t. catenata	X					X		X												
t. utahensis				X																
coloradensis		X						X	X											
piute																				

[1] Refer to Table 3 for explanation of code for drainage systems. An "X" in any column denotes occurrence of a taxon in the mountain range or system represented.

For example, the geographical distribution of N. gouleti n. sp. (Fig. 383) is Nearctic, apparently confined to the Columbia River Basin and its mountainous rim in central Idaho, northeastern and northcentral Oregon and southeastern and southcentral Washington. These general range characteristics for each taxon are summarized with its description (section 3.43).

Size (maximum linear extent) of the range of each species-group taxon was estimated by measuring the straight-line distance between the two most distant localities on the dot map. As discussed below in section 4.22, interspecific differences in range size are extreme, ranging from an estimated 22,550 km for the Holarctic N. gyllenhali (Schönherr) (Fig. 388) to no range (arbitrarily recorded as 1 km) for several taxa known only from a single locality (e.g. N. navajo n. sp., Fig. 400). Refer to Table 6 for a summary of these data. The distributions of taxa were also characterized as to their probable relative continuity or discontinuity (i.e. presence of significantly disjunct populations). For example, the range of N. pallipes (Fig. 396) is relatively continuous, with few significant gaps between localities except those due possibly to gaps in collecting. The known range of N. suturalis (Fig. 398), however, is grossly discontinuous, with a minimum gap of about 2200 km between eastern and western populations; and this hiatus is almost certainly due to inadequate collecting. In those taxa with relatively discontinuous ranges, the polarity of disjunctions was also recorded. For example, as noted above, a major east/west disjunction is evident in the range of N. suturalis; but several significant north/south disjunctions are also apparent. These

Table 5. Geographical relations of Nearctic Nebria taxa: sympatry, parapatry, and allopatry.

Name of taxon	Taxa 01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
01 virescens		M	M	M					m	M	M	M			M	M	M	m	M				M
02 paradisi	M		M	M					m		M					m		M					
03 gouleti	M	M		m					M	M	m					M		m					M
04 hudsonica	M	M	m				M			m	m		m	m		M		m					m
05 l. lacustris											M												
06 l. bellorum																							
07 n. nivalis											m			m		M		M					
08 n. gaspesiana											m												
09 c. crassicornis	m	m									M					m	M	m					
10 c. intermedia	M		M	m							m			M		M		m					M
11 gyllenhali castanipes	M	M	m	m	M		m	m	M	m				M		M		m					
12 g. lassenensis	M														M	M		M					
13 g. lindrothi				m																			m
14 frigida				m			m				M					M		m			M		

Table 5. (continued)

Name of taxon	Taxa																						
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
01 virescens									M			M	M			m	M	M	M	M			
02 paradisi									M				M			M			M				
03 gouleti									m				m			m		m	M				M
04 hudsonica	m		m		m			M	m				m			m		m					
05 l. lacustris								M			m												
06 l. bellorum										m	m												
07 n. nivalis								M	m				M					m					
08 n. gaspesiana								m															
09 c. crassicornis									M				M			M			m				
10 c. intermedia			m	m	m	m		M	m				M			M		m					M
11 gyllenhali castanipes	m				m			m	m		M		M			M		m	M				m
12 g. lassenensis												M	M			M			M	m			
13 g. lindrothi								m	m														
14 frigida	M								M				M					M					

Table 5. (continued)

Name of taxon	Taxa 47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
01 virescens	M	M	M	M	m	M	M		M	M	M	M		M								
02 paradisi		M				m			M			m	m	M								
03 gouleti		M				M								M								
04 hudsonica		M				M			m					m	m	m	m	m			m	
05 l. lacustris																						
06 l. bellorum																						
07 n. nivalis									m													
08 n. gaspesiana																						
09 c. crassicornis	m	m				m			M			m		m								
10 c. intermedia	M					M			M					M	M	M		m				
11 gyllenhali castanipes						M			m					M	m	m						
12 g. lassenensis				M	m	M					M		M	M								
13 g. lindrothi																	m	m	m		m	
14 frigida									M													

Table 5. (continued)

Name of taxon	Taxa 01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
15 lyelli	M											M											
16 a. acuta	M	m	M	M			M		m	M	M	M						m					
17 a. quileute									M									m					
18 s. sahlbergii	m	M	m	m			M		m	m	m	M		m		m	m				m	M	
19 s. modoc	M																						
20 s. triad																							
21 gregaria														M				m					
22 charlottae																		M					
23 a. arkansana				m									m										
24 a. edwardsi	M		M	m					M	M	m			M				p					
25 a. oowah													m										
26 a. uinta				m						m													
27 f. fragilis										m													
28 f. teewinot				m						m	m												

Table 5. (continued)

Name of taxon	Taxa 24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
15 lyelli																M				M			
16 a. acuta									M			M	m			m		m		m			
17 a. quileute													m			M							
18 s. sahlbergii	p							M	m				m			m	M	m	m				
19 s. modoc									M														
20 s. triad																m					m		
21 gregaria																							
22 charlottae													M				M						
23 a. arkansana								m	m														
24 a. edwardsi					p			M	m				M			M		m					
25 a. oowah																							
26 a. uinta				p					M														
27 f. fragilis			p						M														
28 f. teewinot	p							m	m														

Table 5. (continued)

Name of taxon	Taxa 47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
15 lyelli				m	m						m											
16 a. acuta	m	m			m	m			m			m	m	m								
17 a. quileute	m				M			m	m			m		M								
18 s. sahlbergii	m	m				m		m	m			M	M	m	m							
19 s. modoc																						
20 s. triad																						
21 gregaria									m													
22 charlottae																						
23 a. arkansana																	m	m	m		m	
24 a. edwardsi									m					M	m				m			
25 a. oowah																			m			
26 a. uinta																		m				
27 f. fragilis																		m				
28 f. teewinot																m					m	

Table 5. (continued)

Name of taxon	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
	Taxa																						
29 z. zioni										m													
30 z. oasis																							
31 suturalis				M	M		M	M		m	m		m					M					m
32 obliqua	M	M	m	m			m		M	m	m		m	M				m	M				m
33 appalachia					M	n																	
34 pallipes					m	m					M												
35 darlingtoni	M																						
36 mannerheimii	M	M	m	m			M		M	M	M	M		M		m	m	m				M	
37 desolata																							
38 navajo																							
39 eschscholtzii	m	M	m	m					M	M	M	M			M	m	M	m		m			
40 diversa	M																	M				M	
41 g. gebleri	M		m	m			m			m	m			M		m		m					
42 g. cascadensis	M	M	M						m		M	M						m					

Table 5. (continued)

	Taxa																						
Name of taxon	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
29 z. zioni									m					M									
30 z. oasis																							
31 suturalis	M				m				M		M							M					
32 obliqua	m		M	M	m	m		M					m	M		m		m	M	M		M	M
33 appalachia											m												
34 pallipes								M		m													
35 darlingtoni																m				m			
36 mannerheimii	M								m							m	M	M	m				
37 desolata									M														
38 navajo																							
39 eschscholtzii	M								m			m	m				m	M	m	m	m	M	
40 diversa													M			m							
41 g. gebleri	m							M	m				M			M							m
42 g. cascadensis									M				m			m							

Table 5. (continued)

Name of taxon	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
29 z. zioni																		m				m
30 z. oasis																						
31 suturalis									M						M	M	m	m				
32 obliqua	M				M	M			m					m	m	m	m	m	M		M	M
33 appalachia																						
34 pallipes																						
35 darlingtoni					M																	
36 mannerheimii	M	M				m		M	m			m	M	m								
37 desolata																		M				
38 navajo																						
39 eschscholtzii	M	M	M	M	M	M		M	m	M	M	M	M	m								
40 diversa																						
41 g. gebleri	M					M			m					M	m							
42 g. cascadensis		M				m		M	m			m	M	m								

Table 5. (continued)

Name of taxon	Taxa 01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
43 g. rathvoni	M											m			M	m							
44 g. siskiyouensis																				m			
45 g. strawberriensis																							
46 carri			M							M	m												
47 k. kincaidi	M								m	M						m	m	m					
48 k. balli	M	M	M	M					m							m		m					
49 s. spatulata	M																						
50 s. sierrae	M											M			m								
51 ovipennis	m											m			m	m							
52 m. meanyi	M	m	M	M					m	M	M	M				m		m					
53 m. lamarckensis	M																						
54 m. sylvatica																	m	m					
55 metallica	M	M		m			m		M	M	m			M		m	m	m					
56 i. ingens	M																						

Table 5. (continued)

Name of taxa	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
43 g. rathvoni									M			m				m							
44 g. siskiyouensis																m							
45 g. strawberriensis									M							M							
46 carri	m								M									m					
47 k. kincaidi									M				M			M		M					
48 k. balli													M			M			M				
49 s. spatulata																M				M			
50 s. sierrae																M				M			
51 ovipennis									M			M				M				m			
52 m. meanyi									M				m			M		M	m				
53 m. lamarckensis																							
54 m. sylvatica													M			M			M				
55 metallica	m							M	m				m			m		m	m				
56 i. ingens																			M	M			

Table 5. (continued)

Name of taxon	Taxa 47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
43 g. rathvoni			M	M	m					M	M											
44 g. siskiyouensis																						
45 g. strawberriensis																						
46 carri																						
47 k. kincaidi						m	m		M			M		M								
48 k. balli						m			M			M	M	m								
49 s. spatulata					m					m												
50 s. sierrae					m		m			m	m											
51 ovipennis			m	m			m			m	m											
52 m. meanyi		m							m			m	m	m								
53 m. lamarckensis	m			m	m					m												
54 m. sylvatica									M			M		M								
55 metallica	m	m	M			m						M	M	m	m							
56 i. ingens			m	m	m		m															

Table 5. (continued)

Name of taxon	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
	Taxa																						
57 i. riversi	M											M			m								
58 v. vandykei	M	m							m							m	m	M					
59 v. wyeast	M	m										M				m		M					
60 piperi	M	M	M	m					m	M	M	M				m	M	m					
61 s. schwarzi				m						M	m							m					
62 s. beverlianna				m						M	m												
63 purpurata				m									m										m
64 t. trifaria				m						m			m										m
65 t. catenata													m										m
66 t. utahensis																							
67 coloradensis				m									m										m
68 piute																							

Table 5. (continued)

Name of taxon	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
	Taxa																						
57 i. riversi																M				M			
58 v. vandykei													m			M			m				
59 v. wyeast																M			M				
60 piperi	M								m				m			m		M	m				
61 s. schwarzi	m							M	m				m			m			m				
62 s. beverlianna					M			M	m														
63 purpurata								m	m														
64 t. trifaria	m		m	m	m	m		m	m					M									
65 t. catenata		m							M														
66 t. utahensis																							
67 coloradensis									M														
68 piute						m			M														

Table 5. (continued)

Name of taxon	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
57 i. riversi				m	m																	
58 v. vandykei	M	M				m		M	M					m								
59 v. wyeast		M				m			M					M								
60 piperi	M	m				m		M	m			m	M									
61 s. schwarzi									m													
62 s. beverlianna																		m				
63 purpurata																		m	m		m	
64 t. trifaria																m	m				p	
65 t. catenata																	m					
66 t. utahensis																						
67 coloradensis																	m	p				
68 piute																						

Abbreviations used: M = macrosympatric; m = microsympatric; p = parapatric; blank = allopatric

Table 6. Maximum linear extent of geographical range of Nearctic *Nebria* taxa.

Name of taxon	Maximum linear extent of range[1,2] Subspecies	Species
virescens		940
paradisi		320
gouleti		685
hudsonica		3350
l. lacustris	2160	2160
l. bellorum	60	
n. nivalis	15891[3]	17100[3]
n. gaspesiana	1585	
c. crassicornis	350	2830
c. intermedia	2830	
gyllenhali castanipes	6900	22550[3]
g. lassenensis	720	
g. lindrothi	685	
frigida		4870[3]
lyelli		1[4]
a. acuta	3330	3330
a. quileute	60	
s. sahlbergii	4090	4160
s. modoc	60	
s. triad	30	
gregaria		1540
charlottae		1[4]
a. arkansana	650	3390
a. edwardsi	2500	
a. oowah	1[4]	

Table 6. (continued)

Name of taxon	Subspecies	Species
a. uinta	220	
f. fragilis	170	555
f. teewinot	150	
z. zioni	157	185
z. oasis	1[4]	
suturalis		4030
obliqua		4440
appalachia		150
pallipes		2240
darlingtoni		20
mannerheimii		2870
desolata		110
navajo		1[4]
eschscholtzii		1800
diversa		1740
g. gebleri	2400	3100
g. cascadensis	800	
g. rathvoni	650	
g. siskiyouensis	80	
g. strawberriensis	1[4]	
carri		240
k. kincaidi	1280	1570
k. balli	170	
s. spatulata	50	280
s. sierrae	200	
ovipennis		480
m. meanyi	2390	3000

Table 6. (continued)

Name of taxon	Subspecies	Species
m. lamarckensis	20	
m. sylvatica	185	
metallica		5160
i. ingens	90	200
i. riversi	30	
v. vandykei	315	550
v. wyeast	130	
piperi		2060
s. schwarzi	370	1330
s. beverlianna	1[4]	
purpurata		530
t. trifaria	960	1390
t. catenata	660	
t. utahensis	1[4]	
coloradensis		200
piute		20

[1] Linear distance between the two most distant localities in the geographical range of a taxon.

[2] All distances given in kilometers.

[3] Linear range includes populations in Palaearctic Region.

[4] Taxon known only from a single locality; linear range arbitrarily assigned a value of 1 km.

Table 7. Size and orientation of significant disjunctions[1] in the geographical ranges of Nearctic Nebria.

Name of taxon	(1) Distance (km)	(2) Orientation	(3) Nature of Intervening area[2]
virescens	300	N/S	1
paradisi	100	N/S	r
hudsonica	220	N/S	1
	960	E/W	p
l. lacustris	580	E/W	p
n. nivalis	300	N/S	w
	500	E/W	w
n. gaspesiana	300	N/S	1
	700	E/W	w
c. crassicornis	150	E/W	1
c. intermedia	130	N/S	1
gyllenhali castanipes	870	E/W	p
	880	E/W	p
frigida	360	E/W	w
a. acuta	290	N/S	1
	300	N/S	1

Table 7. (continued)

Name of taxon	(1)	(2)	(3)
s. sahlbergii	170	E/W	w
gregaria	170	E/W	w
a. arkansana	140	N/S	1
a. edwardsi	190	N/S	1
suturalis	1300	E/W	1
	1800	E/W	1
obliqua	200	E/W	1
appalachia	80	N/S	1
desolata	65	E/W	1
eschscholtzii	230	N/S	1
diversa	560	N/S	w
carri	210	E/W	1
k. kincaidi	150	E/W	w
k. balli	100	N/S	r
m. meanyi	290	N/S	1
m. sylvatica	120	N/S	w
metallica	430	E/W	w
v. vandykei	190	E/W	1
v. wyeast	90	N/S	1
piperi	330	N/S	r
purpurata	140	N/S	1
t. trifaria	260	E/W	1

Table 7. (continued)

Name of taxon	(1)	(2)	(3)
	280	E/W	1
t. catenata	460	N/S	1
coloradensis	90	N/S	1
	100	E/W	1

[1] I suggest that disjunctions noted here represent actual discontinuities in distributions rather than inadequate regional sampling.

[2] Code used in characterizing intervening areas is as follows:

l = lowland area, any type; p = open prairie; r = river, forming a divide; w = water, sea between island and mainland.

data are considered in the zoogeographic discussion below and in Table 7.

Data on geographical relations (i.e. sympatry, etc.) between the range of one taxon and those of others were also used in considerations of the probable status of various populations of the taxon. For example, the geographical ranges of N. gouleti n. sp. (Fig. 383) and N. hudsonica (Fig. 384) overlap narrowly in certain areas of Washington and Idaho. Slight differences in external structural characters among members of allopatric populations of each are maintained among members of sympatric populations, supporting the hypothesis that these two taxa are distinct species. These data are summarized in Table 5.

With few exceptions, I am confident that the known geographical distributions of Nearctic Nebria closely approximate their true ranges. Certain areas in North America remain inadequately sampled or completely unsampled for Nebria and other carabids. These areas are discussed in section 5.1 under suggestions for future study. I should also note that the distributions of Nebria taxa are known at present only from observations of adults. Because migratory activity is neither known nor likely (except for slight seasonal microhabitat shifts) in Nebria members, and because adults and immatures seem to occupy the same or adjacent microhabitats, range estimates based on adults would not be altered or improved by inclusion of observations on other life stages.

3.23 Natural history

The data and discussions presented in this section represent a first attempt at a comparative natural history of Nearctic Nebria. Topics covered in this section are diverse and include those normally considered under the heading "biology" or "bionomics." Data from the literature and from my own field and laboratory observations have been integrated to present a detailed review of present knowledge on Nebria species. Unequal coverage of various topics is due to great gaps in comparative data on the natural history of Nearctic taxa. At present, data on some topics (e.g. flight, population size and density, etc.) are so random and sparse that no comparative study of these is yet possible. In such instances, data are presented descriptively (rather than comparatively) in the hope that these few details will encourage others to gather additional pertinent data.

One of the stated aims of this project has been to acquire a broad data base, using a variety of character systems, with which to reconstruct cladistic relationships among the Nearctic taxa. These relationships, in turn, serve as the bases for the classification provided (section 3.32). Of the natural history data presented, only those on habitat distribution and life history represent a sufficient number of Nearctic taxa to be of use at present in the study of relationship and, therefore, contribute to the classification. These same data supplement geographical distribution data in both contemporary and historical zoogeographic analyses (section 4.2 below) and contribute to a more detailed picture of the spatial and, to some extent, temporal distributions of these beetles at present and in the

past.

I hope that detailed data on the preferred macro- and microhabitats of members of each taxon (provided under the descriptions of the taxa, section 3.43, but surveyed here) will be of use to paleontologists in reconstructing past regional environments and biotas, and to anyone interested in collecting and/or observing individuals of a particular taxon.

3.231 Habitat distribution

For convenience, I have divided the discussion of habitat distributions among Nebria into two parts: macrohabitat range (gross altitudinal and/or life zone ranges) and microhabitat preference (the range of local conditions preferred by individuals within the macrohabitat range). Although this distinction is at times arbitrary, it facilitates comparisons among different taxa and has permitted organization of data into a form easily handled in zoogeographic analyses.

3.2311 Macrohabitat

Nearctic Nebria are a predominantly montane group. Of the 68 taxa recognized here, 50 (75%) are restricted to montane regions and habitats; six (eight percent) are restricted to mountains in southern parts of their ranges but are more widely distributed in northern parts; seven (10%) occupy low-altitude montane habitats and also range broadly in lowlands; two (three percent) occupy far-northern lowland and low-altitude montane habitats; and two (three percent are restricted to non-montane habitats. The habitat distribution of

N. charlottae Lindroth is unknown.

In montane regions, all Nebria taxa occupy more or less restricted altitudinal ranges; and where the geographical ranges of several species overlap, striking altitudinal zonation patterns are evident (see section 4.22 below for discussion). For example, Fig. 443 illustrates the respective altitudinal ranges of several taxa and the resultant zonation pattern in the Front Range, Colorado. However, the habitat distributions of taxa with latitudinally- or longitudinally-extended ranges cannot be characterized by reference to altitudinal range data alone because their respective altitudinal ranges change with geographical location. As discussed below (section 4.22), altitudinal range of a given taxon is, in most instances, lowered either with increased latitude or with transition from regions of continental to more maritime climate (e.g. a coastward shift in longitude). Figures 355 - 358 graphically illustrate altitudinal shifts with latitude shifts within the ranges of certain taxa. This phenomenon was first noted in scientific literature early in the 1800's (e.g. von Humbolt and Bonpland, 1805). Further investigation (e.g. by Allen, 1871, and Merriam, 1892, 1894a, 1894b, 1898) of this relationship between altitude and latitude or, to some degree, longitude in the distributions of certain organisms and biotas led to formulation of various life zone concepts. Although recognized today as over-simplifications of complex interactions between organisms and their time- and space-extended environments, life zone concepts can be useful tools in facilitating brief characterizations of macrohabitat distributions of taxa. I have found them extremely useful in describing Nebria distributions because life zone concepts

can be applied equivalently throughout geographical ranges of taxa while altitudinal characterizations apply only locally (Kavanaugh, in press [A]). Local differences in topography or exposure also affect altitudinal ranges of taxa, further confounding their characterization by altitude.

Life zones concepts used here are those of Merriam (1892, 1894a, 1898). Those zones occupied by members of one or more *Nebria* taxon include the Upper Sonoran ("Upper Austral"), Transition, Canadian, Hudsonian, and Arctic/Alpine zones. Other regional life zone classifications have been proposed (e.g. that of Ramaley, 1907 [see also Marr, 1967], for the Front Range, Colorado). These apply more precisely within the area of their intended coverage but are not more generally applicable. Merriam life zones are most easily recognized by the conspicuous and/or abundant plant species present (especially the trees); and although species composition of the different zones changes with geography, ambience and climate of respective zones are relatively constant. For example, the Hudsonian zone can be characterized by the presence of Engelmann Spruce (*Picea engelmannii* Engelm.) and Subalpine Fir (*Abies lasiocarpa* Nutt.) in the Front Range, Colorado, but by Mountain Hemlock (*Tsuga mertensiana* Sarg.) and Whitebark Pine (*Pinus albicaulis* Engelm.) in the Sierra Nevada, California. In both areas, however, the subalpine-parkland nature of the zone is maintained.

Life zone distributions of Nearctic *Nebria* taxa are summarized in Table 8. Variation in the range of life zones occupied by members of different taxa is extreme. For example, *N. paradisi* members are restricted to the Arctic/Alpine zone and those of *N. gouleti* to the

Upper Sonoran and Transition zones, while members of *N. gyllenhali lindrothi* n. ssp. occupy a range from the Arctic/Alpine to the Transition zone. The relationship between life zone and geographical ranges is discussed in section 4.22 and illustrated in Fig. 436.

Life zone ranges appear to be continuous in all taxa. No taxa exhibit 'disjunct distributions' with respect to life zone range, as was suggested by Armin (1963) for *N. suturalis* ("*N. longula* LeConte") in the Front Range. Also, no shifts in life zone range with geography are apparent among Nearctic taxa except in *N. purpurata* LeConte (Figs. 358, 409). Members of this species are restricted to the Arctic/Alpine and Hudsonian zones in northern Colorado, to the Hudsonian and Canadian zones in southern Colorado, and to the Transition zone in northern New Mexico (Kavanaugh and Martinko, 1972) --a complete reversal of the usual relationship of increased range altitude with a decrease in latitude (see section 4.23 for discussion).

I assume that present macroclimatic ranges of taxa are determined by intrinsic tolerance limits of their members for one or more environmental factors (e.g. temperature, humidity, etc.), but that present geographical ranges result from the interplay of both time- and space-extended effects of these intrinsic constraints and various historical events (e.g. the existence of past barriers to distributions, glaciations, etc.). Factors affecting geographical distribution are therefore potentially more diverse and difficult to isolate. Attempts to relate the macrohabitat distributions (ranges) of *Nebria* taxa to their respective tolerance limits for certain environmental factors, however, are limited mainly by the paucity of detailed environmental data available. With such data and existing

Table 8. Life zone distributions of Nearctic Nebria taxa.

Name of taxon	Life zone[1] A/A	H	C	T	US	?[4]
virescens	(X)[2]	(X)	X	X		
paradisi	X					
gouleti				X	X	
hudsonica			X	X		
l. lacustris			(X)	X	X	
l. bellorum			X			
n. nivalis	X	X				
n. gaspesiana	X	X				
c. crassicornis	X	X	(X)			
c. intermedia	X	X	(X)			
gyllenhali castanipes	(X)	X	X	(X)		
g. lassenensis		X				
g. lindrothi	X	X	X	X		
frigida	X	X				
lyelli	X					
a. acuta	X	X	X			
a. quileute		X	X			
s. sahlbergii		X	X	(X)		
s. modoc			X	(X)		
s. triad			X	(X)		
gregaria		X[3]				
charlottae						X

Table 8. (continued)

Name of taxon	Life zone A/A	H	C	T	US	?
a. arkansana	X	X	X			
a. edwardsi		X	X			
a. oowah			X			
a. uinta			X	(X)		
f. fragilis			X	(X)		
f. teewinot		(X)	X			
z. zioni			X	(X)		
z. oasis			X	(X)		
suturalis	X					
obliqua		(X)	X	X	X	
appalachia			X	(X)		
pallipes			(X)	X	X	
darlingtoni			(X)	X		
mannerheimii			X	(X)		
desolata					X	
navajo					X	
eschscholtzii				X	X	
diversa			X[2]			
g. gebleri		(X)	X	(X)		
g. cascadensis		(X)	X	(X)		
g. rathvoni		(X)	X	(X)		
g. siskiyouensis			X	(X)		

Table 8. (continued)

Name of taxon	Life zone A/A	H	C	T	US	?
g. strawberriensis			X			
carri		X				
k. kincaidi		X	X			
k. balli		X	(X)			
s. spatulata	X	X				
s. sierrae	X	X				
ovipennis	(X)	X	X			
m. meanyi	(X)	X	(X)			
m. lamarckensis	(X)	X	(X)			
m. sylvatica			X			
metallica		X	X			
i. ingens	X					
i. riversi	X					
v. vandykei	X	(X)				
v. wyeast	X	(X)				
piperi		X	X			
s. schwarzi		(X)	X			
s. beverlianna			X			
purpurata	X	X	X	X		
t. trifaria	(X)	X	X	X		
t. catenata	(X)	X	X	X		
t. utahensis				X		

Table 8. (continued)

	Life zone					
Name of taxon	A/A	H	C	T	US	?
coloradensis	(X)	X	(X)			
piute		X	X			

[1]Life zones abbreviated as follows: A/A = Arctic/Alpine Zone; H = Hudsonian Zone; C = Canadian Zone; T = Transition Zone; and US = Upper Sonoran Zone; modified from Merriam, 1894 and 1898.

[2]Parentheses around an entry denote occurrence of few individuals in a particular zone, or only partial occupation of the zone (i.e. upper or lower extreme only) by taxon members.

[3]For taxa restricted to seacoast habitats, designations of life zones occupied are relatively arbitrary, but represent reasonable approximations of macrohabitat equivalence.

[4]Life zone distribution unknown.

knowledge of macrohabitat distribution, the tolerance limits of these taxa could be estimated. Figs. 355 - 358 illustrate a crude graphic attempt to estimate temperature tolerance limits of several taxa by plotting the altitudinal and latitudinal co-ordinates of their respective distributions and relating these to certain isotherms for mean annual air temperature (generalized temperature data from Mani, 1962 and 1968). This particular temperature character was chosen only because rough data were available. Nonetheless, restriction within a limited (but unspecified) temperature range is indicated, for example, by the distribution of N. obliqua (Fig. 357), perhaps with some shift in tolerance with shift in latitude. Detailed and meaningful analyses must await better climatic data.

One interesting effect of human environmental alteration on the macrohabitat (and geographical) distributions of certain Nearctic Nebria taxa deserves comment here. I have frequently collected members of certain species along streams under bridges at elevations well below the life zone range normally occupied by these species. In fact, individuals were not seen at these elevations except under bridges. Apparently, these cool, shaded, man-made habitat 'islands' may be routinely populated and/or repopulated by downstream drift from life zones above; and there is reason to suspect that small, resident populations can become established in these areas. The short-term result of this 'trollism' is an artificial extension of macrohabitat and, in some instances, the geographical ranges of the taxon. Possible long-term effects are discussed in section 3.234.

3.2312 Microhabitat

Within macrohabitat ranges occupied by members of different Nebria taxa, individuals are found only in a limited subset of available microhabitats. I have attempted to characterize the microhabitats preferred according to type (e.g. stream bank, glacial margin, closed forest, etc.), size, substrate, cover size and type, vegetation, exposure and moisture. Many of my findings agree with those of Lindroth (1961) for the taxa he considered. Other published notes relating to microhabitat preferences in Nearctic Nebria species include the following: Spence (1974), for N. lacustris lacustris Casey and N. pallipes; and Blake (1945), for N. trifaria trifaria. Andersen (1968), Greenslade (1968), Kryzhanovski and Molodova (1973), Lindroth (1965) and Shilenkov (1974) published notes on microhabitats for Palaearctic members of N. gyllenhali. Shilenkov included data on N. nivalis nivalis in far-eastern Asia. Microhabitat preferences for N. brevicollis, the type species of Nebria, have been well-documented (see Greenslade, 1963a, 1963b and 1968; Richards, 1946; Schiller, 1973; Schiller and Weber, 1975; and Thiele, 1968 and 1969a).

Microhabitat preferences of adults and immatures are, in most instances, apparently identical. In the following discussions and in taxon descriptions (section 3.43), statements about microhabitat can therefore be assumed to refer to all life stages unless otherwise noted. Data are summarized in Tables 9, 10, and 11.

Microhabitat type

Habitat types occupied by at least some members of Nearctic taxa include the following: (1) banks of streams, lakes and ponds;

(2) margins of glaciers and snowfields; (3) sea strands; (4) forests; (5) meadows; (6) arctic and alpine tundras; and (7) fellfields and talus slopes. Table 9 summarizes known microhabitat spectra preferred by members of Nearctic Nebria taxa. Only N. charlottae remains uncharacterized in its habitat preferences.

Riparian habitats.--Members of 63 taxa (93% of the fauna) are riparian (i.e. prefer stream banks or the shores of lakes or ponds) at least in part. Members are strictly riparian in 31 taxa (46%), riparian except at upper altitudinal range limits in 13 taxa (19%), riparian only at lower altitudinal range limits in 13 taxa (19%), facultatively riparian in six taxa (nine percent), and non-riparian in four taxa (six percent). Members of seven taxa, including N. lacustris lacustris and N. pallipes, are commonly collected on the banks of lakes and ponds as well as streams, while members of the remaining riparian taxa are restricted to, or common only on, stream banks. In general, there is an inverse relationship between altitude and the degree to which members of a taxon are restricted to riparian habitats (see further discussion below in this section).

Organisms which occupy stream banks (e.g. members of most Nebria taxa) must face seasonal and/or catastrophic changes in water levels which result in inundation of the banks. Beetles may be drowned or swept downstream from suitable habitats. Andersen (1968) discussed inundation of riparian habitats and responses of organisms (including members of N. gyllenhali) to these events. Spence (1974) noted downstream drift of adults and larvae of N. lacustris lacustris and N. pallipes as a result of increased runoff after rains. It can be

Table 9. Microhabitat distributions of Nearctic <u>Nebria</u> taxa.

Name of taxon	Microhabitat type[1]								
	O	S	L	M	F	Tu	Ta	N	?[3]
virescens				X	X		X	X	
paradisi						X		X	
gouleti		X							
hudsonica		X							
l. lacustris		X	(X)[2]						
l. bellorum		X							
n. nivalis		X				(X)		X	
n. gaspesiana		X					X	X	
c. crassicornis		(X)	(X)	X	(X)	X		X	
c. intermedia		(X)	(X)	X	(X)	X		X	
gyllenhali castanipes		X	X	X	X	X			
g. lassenensis				X	(X)				
g. lindrothi		X	X	X	X	X	(X)	(X)	
frigida		X				X		(X)	
lyelli		X					X	X	
a. acuta		X						X	
a. quileute		X							
s. sahlbergii		X						(X)	
s. modoc		X							
s. triad		X							
gregaria	X								
charlottae									X

Table 9. (continued)

Name of taxon	Microhabitat type								
	O	S	L	M	F	Tu	Ta	N	?
a. arkansana		X					(X)	(X)	
a. edwardsi		X							
a. oowah		X							
a. uinta		X							
f. fragilis		X							
f. teewinot		X							
z. zioni		X							
z. oasis		X							
suturalis						(X)	X	X	
obliqua		X							
appalachia		X							
pallipes		X	X						
darlingtoni		X							
mannerheimii		X							
desolata		X							
navajo									X
eschscholtzii		X							
diversa	X								
g. gebleri		X							
g. cascadensis		X							
g. rathvoni		X							
g. siskiyouensis		X							

Table 9. (continued)

Name of taxon	Microhabitat type O	S	L	M	F	Tu	Ta	N	?
g. strawberriensis		X							
carri		X			(X)				
k. kincaidi		X			(X)				
k. balli		X			(X)				
s. spatulata		X					X	X	
s. sierrae		X		(X)			X	X	
ovipennis		X		(X)			X	(X)	
m. meanyi		X						X	
m. lamarckensis		X							
m. sylvatica		X							
metallica	X	X		(X)					
i. ingens		X					X	X	
i. riversi		X					X	X	
v. vandykei		(X)						X	
v. wyeast		(X)						X	
piperi		X							
s. schwarzi		X							
s. beverlianna		X							
purpurata		X					X	X	
t. trifaria		X	X	X	X	X		(X)	
t. catenata		X	X	X	X				
t. utahensis									?

Table 9. (continued)

Name of taxon	Microhabitat type O	S	L	M	F	Tu	Ta	N	?
coloradensis		X		(X)	(X)				
piute		X		X	X				

[1]Microhabitat types abbreviated as follows: O = open seacoast, in supralittoral zones; S = streambanks; L = banks of lakes or ponds; M = meadows; F = forest; Tu = tundra; Ta = talus slopes; N = perinival areas, margins of glaciers or snowfields.

[2]Parentheses around an entry denote what I consider an uncharacteristic occurrence for members of a particular taxon.

[3]Microhabitat distribution unknown.

Table 10. Data on characteristics of microhabitats preferred[1] by members of Nearctic <u>Nebria</u> taxa, I. Association with water bodies (including streams, lakes, oceans, snowfields, or glaciers).

Name of taxon	(1) Size of water body (A) stream	(B) lake or pond	(C) ocean or sea	(D) snowfield	(E) glacier	(F) unassociated	(2) Distance to water body (A) stream or lake	(B) snow or ice	(C) ocean or sea	(D) unassociated
virescens	1-3[2]			1-3		X	2-6	4-6		X
paradisi				1-3	X			1-5		
gouleti	3-8						1-5			
hudsonica	2-8						1-5			
l. lacustris	2-8	1-5					2-4			
l. bellorum	2-5						2-5			

Table 10. (continued)

	(1)						(2)			
Name of taxon	(A)	(B)	(C)	(D)	(E)	(F)	(A)	(B)	(C)	(D)
n. nivalis	3-4			1-2			1-4			
n. gaspesiana	2-6			1-2		(X)[3]	1-3	1-5		(X)
c. crassicornis	(6)			1-3		X	(1-6)			X
c. intermedia	(3-5)	(2-4)				X	(2-6)	1-6		X
gyllenhali castanipes	2-7	2-4				X	1-6	1-6		X
g. lassenensis	2	2				X	2-6			X
g. lindrothi	1-6	1-2		2		X	1-6	1-6		X
frigida	3-7			1		X	2-6	5-6		X
lyelli	1-3			1-3			1-6	1-6		X
a. acuta	1-6			1-3			0-6	1-6		
a. quileute	4-5						1-4			
s. sahlbergii	3-8		X				1-4		2	
s. modoc	3						1-4			

Table 10. (continued)

Name of taxon	(1) (A)	(1) (B)	(1) (C)	(1) (D)	(1) (E)	(1) (F)	(2) (A)	(2) (B)	(2) (C)	(2) (D)
s. triad	3-5						1-4			
gregaria			X						(2)	
charlottae			unknown					unknown		
a. arkansana	2-4	2					1-5			
a. edwardsi	1-7			1-2			1-4	1-4		
a. oowah	4						1-4			
a. uinta	3-6						1-4			
f. fragilis	3-5						1-4			
f. teewinot	2-6						1-4			
z. zioni	1-6						0-4			
z. oasis	3						0-4			
suturalis	2-3			1-2	X	X	1-6	1-6		X

Table 10. (continued)

Name of taxon	(1) (A)	(1) (B)	(1) (C)	(1) (D)	(1) (E)	(1) (F)	(2) (A)	(2) (B)	(2) (C)	(2) (D)
obliqua	3–8						1–6			
appalachia	3–5						1–5			
pallipes	3–8	1–5					1–6			
darlingtoni	6						1–5			
mannerheimii	5–8						1–6			
desolata	3–5						1–5			
navajo				unknown				unknown		
eschscholtzii	2–8						1–6			
diversa			X						1–2	
g. gebleri	1–7						1–5			
g. cascadensis	2–7						1–6			
g. rathvoni	2–6						1–4			
g. siskiyouensis	5						1–5			

Table 10. (continued)

	(1)						(2)			
	(A)	(B)	(C)	(D)	(E)	(F)	(A)	(B)	(C)	(D)
g. strawberriensis	3–4						1–5			
carri	2–3					(X)	1–6			(X)
k. kincaidi	1–5					(X)	1–4			(X)
k. balli	1–6					(X)	1–6			(X)
s. spatulata	1–3			1–3		X	0–6	1–6		X
s. sierrae	1–3	1		1–3		X	3–6	1–6		X
ovipennis	1–4			(1–3)		X	1–6	1–6		X
m. meanyi	3–6			1–3	X		1–4	1–5		
m. lamarckensis	3–4						0–4			
m. sylvatica	4–5						1–4			
metallica	3–7		X			X	1–6		2–3	X
i. ingens	3–4			1–3			0–4	1–6		
i. riversi	1			1–3			1–5	1–6		

Table 10. (continued)

	(1)						(2)			
	(A)	(B)	(C)	(D)	(E)	(F)	(A)	(B)	(C)	(D)
v. vandykei	4–5			1–3	X		1–3	0–5		
v. wyeast	3–5			1–3	X		1–3	0–6		
piperi	4–7						1–4			
s. schwarzi	6–8						1–5			
s. beverlianna	7						0–5			
purpurata	3–5			1–2		(X)	1–4	4		(X)
t. trifaria	1–7	1–2		(1–3)		X	1–6	1–6		X
t. catenata	1–3	1–2				X	1–6			X
t. utahensis				unknown				unknown		
coloradensis	3–4					(X)	1–5			(X)
piute	1–4			(1)		X	1–6	3–6		X

[1]Data presented here represent my field observations supplemented by selected data from the literature (Edwards, 1975; Lindroth, 1955a, 1961, and 1963a; and Spence, 1974). Most observations were made during daylight hours. "Preferred" microhabitat therefore refers specifically to places where beetles hide during the day (see text for further comment). Ranges in data reflect ranges of observations only; and these are presented as crude estimates of actual preference ranges of taxa.

[2]Code used for data presented here is as follows:

(1) Size of water body. (A) stream: 1=small seep or snowmelt trickle, width (w.) less than 5cm; 2=very small creek (rivulet), w. 5cm to 1 m; 3=small creek, w. 2m to 3m; 4=medium creek, w. 4m to 5m; 5=large creek, w. 6m to 10m; 6=small river, w.15m to 25m; 7=medium river, w. 30m to 60m; and 8=large river, w. greater than 60m. (B) lake or pond: 1=small pond, average diameter (a.d.) less than 30m; 2=small lake, a.d. 30m to 150m; 3=medium lake, a.d. 160m to 1.5km; 4=large lake, a.d. 1.6km to 8 km; 5=very large lake, a.d. greater than 8km. (C) ocean or sea: size unclassified; (D) snowfield: 1=small snowfield, a.d.less than 10m; 2=medium snowfield, a.d. 10m to 60m; 3=large snowfield, a.d. greater than 60m. (E) glacier: size unclassified. An "X" denotes association only, under any of the above headings.

(2) Distance from water body. (A) stream or lake and (B) snow or ice: 0=in or at edge of water or on snow; 1=1cm to 5cm distant; 2=6cm to 15cm distant; 3=16cm to 25cm distant; 4=0.3m to 0.6m distant; 5=0.7m to 4m distant; and 6=more than 4m distant. (C) ocean or sea: 1=at high

tideline; 2=above highest tideline.

[3]Parentheses around an entry denote what I consider an uncharacteristic occurrence for members of a taxon.

Table 11. Data on characteristics of microhabitats preferred[1] by members of Nearctic Nebria taxa, II. Substrate[2], cover type[3], and exposure[4, 5].

Name of taxon	(1) Substrate (A) Alluvium	(B) Moraine	(C) Pyroclastics	(D) Talus	(E) Bedrock	(F) Soil	(G) Leaf litter	(H) Other	(2) Cover type (A) Stones	(B) Logs	(C) Leaf litter	(D) Other	(3) Exposure
virescens					X	X	X			1	X	m	0-3
paradisi			1-2		X	X			1-5				0
gouleti	2-5								2-3				0-2
hudsonica	3-7								1-3				0-3
l. lacustris	2-5								1-2				1-3
l. bellorum	2-5								1-3				2-3
n. nivalis	2-6								2-4				0

Table 11. (continued)

Name of taxon	(1) (A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(2) (A)	(B)	(C)	(D)	(3)
n. gaspesiana	3-6			X					3-4				0-2
c. crassicornis	2-6	X	1			X			2-4	1,2			0-1
c. intermedia	2-6					X			2-4	1,2		m	0-3
gyllenhali castanipes	2-5			X		X	X		2-3	1,2	X		0-3
g. lassenensis						X			2-3				0-3
g. lindrothi	2-5			X		X	X		2-3	1,2	X		0-3
frigida	2					X			1-3	1,2	X		0-2
lyelli		X		X	X				3-5				0
a. acuta	3-6	X	1			X			1-5				0-3
a. quileute	3-6								1-3				3
s. sahlbergii	2-6								1-3	2		d	0-3
s. modoc	3-6								1-3				3

Table 11. (continued)

Name of taxon	(1) (A)	(1) (B)	(1) (C)	(1) (D)	(1) (E)	(1) (F)	(1) (G)	(1) (H)	(2) (A)	(2) (B)	(2) (C)	(2) (D)	(3)
s. triad	3–6								1–3				1–3
gregaria	3–5		1		x				2–5			d	0
charlottae					unknown					unknown			?
a. arkansana	3–6				X	X			1–3				0–3
a. edwardsi	3–6				X	X			1–3				0–3
a. oowah	3–6								1–3				1–2
a. uinta	3–6					X			1–3				1–3
f. fragilis	3–6								1–3				1–3
f. teewinot	2–6								1–4				0–3
z. zioni	1–6								1–3				0–3
z. oasis	3–6				X				1–3				3
suturalis	2–6	X		X	X				1–5				0

Table 11. (continued)

Name of taxon	(1)								(2)				(3)
	(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(A)	(B)	(C)	(D)	
obliqua	1-4								1-3	2			0-3
appalachia	3-6								1-3				3
pallipes	2-6					X			1-3	1,2			1-3
darlingtoni	2-6								1-3				1-3
mannerheimii	1-7								1-4				0-3
desolata	3				X				1-5				3
navajo					unknown					unknown			?
escholtzii	1-7								1-4				0-3
diversa	3									3			0
g. gebleri	2-6					X			1-4				1-3
g. cascadensis	2-6					X			1-4	1,2			1-3
g. rathvoni	3-6								2-4				0-3

Table 11. (continued)

Name of taxon	(1)								(2)				(3)
	(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(A)	(B)	(C)	(D)	
g. siskiyouensis	3–7								2–4				1–3
g. strawberriensis	3–6					X			2–4				3
carri	3–7					X			1–3				2–3
k. kincaidi	3–7					X		b	1–4	1,2		m	3
k. balli	3–6					X		b	2–3	1,2		m	3
s. spatulata	3–6	X		X	X	X			2–5				0
s. sierrae	3–6	X		X	X	X			2–5				0
ovipennis	3–6	X		X	X	X			2–5				0–3
m. meanyi	2–6	X	1						1–5				0–3
m. lamarckensis				X	X				2–5				0
m. sylvatica	3–6								1–4				3
metallica	2–3		1			X			1–3	1,2			0–3

Table 11. (continued)

Name of taxon	(1) (A)	(1) (B)	(1) (C)	(1) (D)	(1) (E)	(1) (F)	(1) (G)	(1) (H)	(2) (A)	(2) (B)	(2) (C)	(2) (D)	(3)
i. ingens				X	X				3–5				0
i. riversi	4–6			X	X				2–5				0
v. vandykei		X	1–2						4–5				0
v. wyeast		X	1						4–5				0
piperi	3–6	X							3–4				0–3
s. schwarzi	2–6								1–3				0
s. beverlianna	3–6								2–4				0
purpurata	3–6				X	X			2–4				0–3
t. trifaria	3–6					X			2–4	2			0–3
t. catenata	3–6					X			2–4	2			0–3
t. utahensis				unknown						unknown			?
coloradensis	3–6					X			2–4				0–3

Table 11. (continued)

	(1)								(2)				(3)
	(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(A)	(B)	(C)	(D)	
piute	3-6					X			2-4	2			0-3

[1]Data presented here represent my field observations supplemented by selected data from the literature (Edwards, 1975; Lindroth, 1955a, 1961, and 1963a; and Spence, 1974). Most observations were made during daylight hours. "Preferred" microhabitat therefore refers specifically to places where beetles hide during the day (see text for further comment). Ranges in data reflect ranges of observations only; and these are presented as crude estimates of actual preference ranges of taxa.

[2]Substrate: material upon which beetles stand or move.

[3]Cover type: material under which beetles hide.

[4]Exposure: degree of exposure of hiding place to direct sunlight.

[5]Code used for data presented here is as follows:

(1) Substrate. (A) Alluvium: 1=clay; 2=silt; 3=fine sand; 4=medium sand; 5=coarse sand; 6=fine to

Table 11. (continued)

medium gravel; 7=coarse gravel. (B) Moraine: unsorted till, material range from silt to boulders; unclassified. (C) Pyroclastics: 1=volcanic ash; 2=pumice lapilli. (D) Talus: unclassified. (E) Bedrock: weathered surface material (<u>in situ</u>); unclassified. (F) Soil: organic; unclassified. (G) Leaf litter: unclassified. (H) Other: b=under loose bark.

(2) Cover type. (A) Stones: 1=average diameter (a.d.) less than 5cm; 2=a.d. 5cm to 15cm; 3=a.d. 16cm to 25cm; 4=a.d. 30cm to 60cm; 5=a.d. greater than 60cm. (B) Logs: 1=fallen twigs, branches, bark chips; 2=trunks of fallen trees; 3=beach driftwood. (C) Leaf litter: unclassified. (D) Other: d=unclassified debris (e.g. discarded, sheet metal, beer cans, lumber, etc.); m=moss or other moist vegetative carpets.

An "X" denotes association only, under any of the above headings.

(3) Exposure: 0=open ground, completely unshaded; 1=open ground, partially shaded during few daylight hours; 2=area shaded during midday; 3=area fully shaded, except perhaps during early morning or late afternoon.

assumed, however, that selective pressures are strong for development of behavior patterns in riparian organisms which optimize avoidance of flooding danger. I have observed such behavior in members of several taxa, including N. eschscholtzii Ménétriés, and N. obliqua (in California and Alberta, respectively). Prior to the onset of the rainy season (winter in California, spring in Alberta), individuals (adults and larvae) disappear from the typical streamside habitat and, presumably, retreat to higher ground. This retreat is well in advance of any actual rise in water level and must be triggered by essentially unrelated environmental events (e.g. change in temperature or photoperiod). T. L. Erwin (personal communication) has observed identical behavior in riparian members of Brachinus species (Brachinida). As discussed below (section 3.233), riparian Nebria are apparently also able to make use of streams for certain activities, such as escape from potential predators and locomotion. Their adaptation to riparian life, therefore, steps beyond pure survival in this habitat toward more complex use of it.

Perinival habitats.--Members of 20 Nearctic Nebria taxa (29% of the fauna) are at least marginally associated with glaciers or snowfields. All members of N. paradisi and most members of N. vandykei, N. ingens, N. spatulata, and N. lyelli are perinival (i.e. prefer areas at the margins of glaciers or snowfields). At the lower altitudinal range limits for the last four taxa, members are riparian in most areas. Members of several other taxa (e.g. N. meanyi meanyi Van Dyke, N. acuta acuta Lindroth, and N. purpurata) are perinival only at the upper latitudinal range limits of their respective taxa.

Lindroth (1965) and Friden (1971) have shown that microclimate even near margins of large glaciers or icefields is much milder (as inferred from the species composition of perinival faunas) than previously assumed. However, members of Nebria taxa which specialize in use of such habitats must possess special behavioral and metabolic adaptations. Mani (1962 and 1968) discussed peculiarities of this environment and the kinds of adaptations to it seen in a variety of perinival insects. Some interesting behavior patterns observed in perinival Nearctic Nebria are discussed below.

Sea strands.--Members of two taxa, N. diversa and N. gregaria, are found only in the supralittoral zone of sea strands. I found members of N. sahlbergii sahlbergii Fischer von Waldheim and N. metallica in this habitat at Cold Bay, Alaska; but members of these taxa are riparian in most other areas sampled.

Forest and meadow habitats.--No Nearctic taxa have members which are restricted to true forest or meadow habitats (i.e. unassociated with some defined water body) although the macrohabitat ranges of most taxa are within forested zones. Members of several taxa are, however, common in moist forest and/or meadow areas. Among these taxa are N. virescens, N. gyllenhali, N. crassicornis Van Dyke, and N. trifaria and its closest relatives. In general, members of these species are riparian at lower altitudinal range limits for their respective taxa. Members of N. spatulata are found in moist, subalpine meadows at the lower altitudinal range limit for the species but completely avoid forested areas. Other taxa whose members are found in meadows (e.g. N. crassicornis, N. gyllenhali, or N. trifaria are also well

represented in moist forest areas at the same or lower altitudes.

As noted above, members of several taxa leave stream banks at certain times (e.g. to avoid possible inundation). Frequently, these beetles enter forest microhabitats and become temporary residents. Members of _N. kincaidi_, for example, are extremely abundant in forests during and just after spring snowmelt. By mid-summer, most individuals have moved to streambanks, where breeding and other life cycle events occur. At least some of these temporary migrations from streambanks by members of certain taxa may reflect a seasonal expansion of suitable microclimatic conditions (e.g. in temperature or moisture) which permits, rather than requires, movement (see also below).

Arctic and alpine tundras.--Members of few Nearctic taxa are found in true tundra habitats unassociated with streams, lakes, glaciers or snowfields. Members of _N. crassicornis_ are most common in alpine tundra habitats, and those of _N. gyllenhali lindrothi_ are as common in these areas as in other habitats. Members of _N. trifaria trifaria_, _N. frigida_, _N. gyllenhali castanipes_ (Kirby) and _N. suturalis_ are found on tundra only in certain geographical areas. For example, members of _N. gyllenhali castanipes_ are restricted to tundra areas on Mount Washington, New Hampshire, but to lower riparian or forest habitats in the Northern Rocky Mountains.

Talus slopes and fellfields.--Members of _N. suturalis_ are common only in these habitats, while those of several other species, including _N. purpurata_, _N. nivalis gaspesiana_, _N. lyelli_, and _N. spatulata_ are found in talus or fell areas but not restricted to them. On the surface, these habitats appear extremely barren and inappropriate for members of

a basically riparian group. However, the depths of these formations often contain flowing water, snow or ice which persists (in what are essentially cold-desert areas) throughout the year and contributes to a stable, favorable environment for Nebria.

Stream size

A relationship was found, in some instances, between size of a stream (measured as stream width) and taxon representation in its riparian Nebria fauna. For example, members of N. piperi Van Dyke, N. schwarzi and N. mannerheimii are found only on the banks of small to large rivers (width from 10m to over 60m) in most areas. Members of N. gebleri cascadensis n. ssp. are common only on the banks of small to large creeks (width from one meter to 10m) at similar altitudes. Few members of N. gebleri cascadensis are found along larger streams (i.e. with members of N. piperi and N. mannerheimii); but these are probably individuals washed out from smaller tributaries. Similar downstream drift may obscure stream size preferences in members of other taxa; and because stream size is generally correlated with altitude (i.e. larger streams at lower elevations), opportunities for valid comparisons of stream size preferences among taxa restricted to mid- and high-altitudes are few.

No clear preferences were recognized among Nearctic taxa with riparian or perinival members in relation to the size of standing water bodies (e.g. lakes, ponds, snowfields, etc.). For example, members of N. pallipes have been collected repeatedly on the shores of small ponds as well as large lakes. Members of N. paradisi and N. vandykei are found at the margins of both very small snow patches and vast

snowfields. Individuals of each appear to be relatively more abundant at the edges of small, isolated snow patches in mid- to late-summer. However, this is probably a concentration effect due simply to shrinkage of the more extensive early-season snowpack, with individuals converging as they follow receding snow margins.

Substrate, cover, exposure and moisture

Diurnal hiding places.--Members of *Nebria* species are most often collected during daylight hours while hiding under cover (e.g. stones or logs). Their apparent preferences for certain diurnal hiding places (characterized by substrate, cover, vegetation, exposure and moisture) are of interest not only to collectors, but also to those interested in how these cool- or cold-adapted nocturnal beetles survive the heat of day. The choice of certain hiding places is really a choice among a spectrum of diurnal microclimatic regimes. Mani (1962 and 1968) discussed (and illustrated) temperature gradients under and around surface cover (e.g. stones) relative to its size, thickness and degree of contact with the substrate. For example, spaces under or between large, thick, deeply-embedded stones provide constant, cool, moist conditions throughout the day, while the same spaces under small, thin, shallowly-embedded stones may be subject to high diurnal temperature and humidity fluctuations. Mani also briefly discussed the characteristics of different substrates in relation to temperature and moisture. Clay and silt, for example, hold more moisture than sand or gravel. However, highest evaporative cooling rates in warm, dry areas (and, therefore, the coolest microhabitats in these areas) are found in sandy substrate.

Observations indicate that Nebria are very efficient "behavioral homeotherms" (that is, they maintain body temperature within a metabolically acceptable range by following temperature gradients and confining themselves to thermally suitable areas (see also below)). I assume, therefore, that homeothermy is a driving force behind observed or presumed preferences for cover, substrate, exposure and moisture. However, selection of a hiding place with certain characteristics may also reflect other requirements (e.g. proximity to foraging areas). Further study is required before apparent preferences can be understood in relation to homeothermy or other demands in Nebria. My field data on N. desolata may, however, provide one example of the manner in which homeothermy is maintained through selection of particular substrate, cover, etc. Members of this species are found during the day only in moist, sandy substrate under sandstone blocks at the undercut bases of cliffs. They avoid all other types of cover (e.g. granite stones) in the area. Temperature data recorded on June 22, 1971 at 15:00 in one locality (see further notes in section 3.43) were as follows: air (at waist height), 33°C; stream, in sun (at 3cm depth), 30°C; stream, in shade of overhanging cliff, 25°C; moist sand in shade, 14°C. This amazing thermal gradient occurred over a linear distance of about two meters and resulted from evaporative cooling in the shaded cliff base. Because sandstone blocks, but not granitic stones, can absorb and release moisture readily and thereby participate in the evaporative cooling process, only the sandstone provided sufficiently cool hiding places for the beetles (see comments of Lindroth, 1949:817). Temperature in the microhabitat occupied by the beetles (i.e. 14°C) was similar to values

recorded in hiding places of members of numerous other taxa in other geographical areas; but other microhabitats in the area described above were too hot.

One implication of the example above is that what are observed as preferences for certain substrate, cover or exposure characteristics might be better interpreted as simple responses to temperature, moisture, or other environmental gradients. However, in the absence of additional detailed environmental data to compare with microdistributional data on taxa, observed 'preferences' are treated as such in the following discussion.

Substrate preferences are evident among members of several Nearctic _Nebria_ taxa, although members of most taxa show no such preferences. Members of _N. diversa_ are found only on coarse sand (under driftwood and other debris on open, sandy ocean beaches). Members of _N. metallica_ and _N. frigida_ are, in most areas, found only on silt substrates, those of _N. piperi_ and _N. desolata_ only on sand. Members of _N. vandykei_ and _N. paradisi_ clearly prefer volcanic ash substrates when these are available; but those of the former taxon prefer morainal substrate (i.e. mixed silt ["glacial flour"], gravel and stones of varying size) at lower altitudes. Members of _N. suturalis_, _N. ingens_, _N. lyelli_ and _N. spatulata_ appear to prefer bare rock substrates and are found most commonly in talus slopes hiding between stones.

Members of _N. virescens_, _N. gyllenhali_ and _N. crassicornis_ are commonly found in forests on organic soil; but neither these nor members of other Nearctic taxa are restricted to this substrate. Members of a majority of taxa are found on a variety of substrates,

dependent on the array available. An altitudinal transect along the course of any stream will generally demonstrate transition, with decreasing altitude, from bare rock, through gravel and sand, to silt and clay as the most common substrate--a fact consistent with details of the erosion cycle. Examples of apparent substrate preference noted above do not include those in which altitudinal range of the taxon significantly restricts the substrate range available. It is often tempting, however, to label instances of differential substrate availability as substrate preferences. For example, members of *N. lacustris lacustris* are found commonly only in sand/gravel substrates at high elevations in the Adirondack Mountains, New York, but on clay/ silt substrates at lower elevations in that state. Members, therefore, occupy a wide range of substrates over the range of the taxon, but appear restricted to certain substrates in certain areas. These apparent local substrate preferences merely reflect differences in the availability of various substrate types at different altitudes.

I have repeatedly observed an interesting behavioral response to disturbance by members of three taxa (*N. acuta acuta*, *N. meanyi meanyi* and *N. vandykei*) commonly found in morainal substrate (at high altitudes). Recent (post-Glacial), barren moraines, especially those being undercut or eroded by streams, are extremely unstable formations of mixed composition (including silt, boulders and particles of intermediate size). Removal of a single stone (or an errant footstep) can initiate substantial slides of this unconsolidated material. Most *Nebria* seek deeper cover when their hiding places (e.g. in talus slopes or on rocky stream banks) are disturbed. When moraines described above are disturbed, however, members of these three taxa immediately begin

to leave their hiding places, often in large numbers, and run on the surface, even in broad daylight. I term this exodus the 'avalanche response' and suggest that it may be highly adaptive for survival in this substrate. The size composition of morainal deposits is such that interstitial spaces normally occupied by the beetles could easily be compressed or filled by small-sized particles during or as a result of landslide, thereby trapping or smashing the beetles. With other cover/substrate combinations (e.g. stones in gravel), interstitial spaces may change position but are not eliminated with disturbance. The 'avalanche response' is therefore viewed as a mechanism to avoid burial in this unique microhabitat.

Preferences for particular type and size of cover are apparently rare among Nearctic _Nebria_ (see Machard, 1970, for brief notes on cover preferences in members of some Palaearctic alpine species). In general, cover of all sizes and types (e.g. stones, logs or other available debris) are used by members of mid-altitude taxa. At lowest altitudes, beetles seek shaded areas (see below) or only larger stones or water-soaked logs. At highest altitudes, larger stones are clearly favored.

Examples of apparent preferences for cover type or size include the following. Members of _N. frigida_ are common, in most areas, only in thin leaf litter or under twigs, bark chips or small logs but not stones. In forests, members of _N. gyllenhali_ are common only under logs and apparently avoid stones in the same but not in other habitats (e.g. members are commonly found under stones along streams). As noted above, members of _N. desolata_ are found only under sandstone blocks and chips and avoid other cover. Members of _N. piperi_ appear to prefer

very large stones adjacent to broad, flat, moist sandy beaches for cover; and those of N. vandykei are most often found under very large and deeply-embedded stones at the margins of snowfields.

Members of most Nearctic taxa are found on barren ground, whether on rocky stream banks, margins of snowfields or in talus slopes. Some members of N. ovipennis, N. gyllenhali and N. crassicornis are found under stones in alpine and subalpine meadows of sparse to dense, low vegetation (e.g. Carex spp., alpine Salix spp.). Members of N. virescens, N. gyllenhali and N. crassicornis are common in forests with sparse to moderately dense understory vegetation; and those of N. frigida are found commonly only under streamside vegetation (Salix, Alnus and Populus spp.), except above or north of treeline.

Preferences for different degrees of exposure are conspicuous only in a few instances. Members of N. gebleri cascadensis, N. kincaidi, N. carri and some other taxa are common only on streambanks which are barren (free of vegetation) but fully-shaded by the adjacent forest canopy. Members of N. desolata are found only in the shade of undercut sandstone cliffs. Nebria inhabiting arctic and alpine areas are subject to extreme exposure. Members of some of these taxa (e.g. N. vandykei) have been found in exposed, but not in shaded, areas below treeline, suggesting an actual preference for the former. Members of most taxa exhibit no clear exposure preference, but rather seek shaded hiding places in warmer areas (e.g. at lower altitudes and latitudes) and more exposed places at upper altitudinal or latitudinal limits for their respective taxa.

Moisture appears to be an extremely important factor in both the macro- and microhabitat distributions of Nebria. Members of most taxa

are closely associated with water bodies (streams, lakes, glaciers, etc.) or at least moist areas (in meadows or forests). Field observations have convinced me, however, that the temperature-modifying effects of these water sources are much more important for *Nebria* than moisture or humidity considerations *per se*. It is possible that moisture may be a critical factor for the egg stage of the life cycle in most or all species; but adults, larvae and pupae exhibit marked independence from water bodies in areas where thermal requirements are otherwise satisfied. For example, members of *N. gyllenhali lindrothi* are restricted to the margins of streams only at low altitudes (ca. 2500m) in the Rocky Mountains of Colorado and New Mexico. At highest altitudes (ca. 3900m) in the same region, members are found on open, dry tundra. Similarly, members of *N. meanyi meanyi* are confined to stream margins at low altitudes (ca. 800m) on Mount Rainier, Washington, but range widely in relation to streams and snowfields at or above timberline there (ca. 1700m). Members of *N. diversa* and *N. gregaria* are found along exceptionally cool stretches of sea coast and have no direct association with the ocean or other water bodies.

Members of all strictly riparian taxa show much more subtle, but equally impressive responses to temperature as modulated by streams. Over a taxon's altitudinal range in a particular area, members are found to occupy hiding places of differing distance from the stream margin, depending on altitude. This distance/altitude relationship is always direct (i.e. increased distance from the water margin with increased altitude). For example, members of *N. hudsonica* are found only within 10cm of stream edges in exposed areas at 2000m in the Front

Range, Colorado, but at distances up to two meters from the water at 3000m on the same streams. Where members of several different species are found together on a streambank, the distances of their respective hiding places from the water almost always reflect (inversely) the altitudinal ranges of their respective taxa--that is, members of taxa with higher altitudinal ranges are found closer to the water at a given altitude than members of taxa with lower altitudinal ranges. Fig. 359 illustrates this relationship using field data on members of *N. hudsonica*, *N. obliqua* and *N. gyllenhali lindrothi* in the Front Range. Spence's (1974) findings for members of *N. pallipes* and *N. lacustris lacustris* in Vermont also reflect this relationship. My interpretation of these and similar findings with other taxa is that temperature rather than moisture is the critical factor limiting microhabitat distribution.

Substrates for nocturnal activity.--Data on substrate preferences during nocturnal activity periods are few. My own field observations (and those of Edwards, 1975, and Spence, 1974) suggest that these beetles are active at night in roughly the same microhabitats in which they take cover during the day, except for perinival forms. Daytime collecting, therefore, gives an approximation of substrate preferences during activity. Perinival beetles are active on the snow surface at night but leave it to hide elsewhere during the day. Table 12 summarizes available data on nocturnal substrate preferences.

In some areas, members of several different taxa are commonly found hiding together under the same stone(s) during the day. The assumption that members of each also prefer similar substrates at night

may be correct in many instances. For example, members of N. paradisi, N. vandykei, N. meanyi meanyi, N. acuta and N. crassicornis are found together under stones in one or another locality, and all are found on snowfields at night. However, preferences for similar diurnal hiding places do not necessarily mean that nocturnal preferences are also identical. At an altitude of 600m on Nisqually River, Mount Rainier, Washington, for example, members of N. acuta acuta, N. mannerheimii, N. piperi, and N. sahlbergii sahlbergii were together hiding under stones within one meter of the stream margin during daylight hours. At night, however, members of these taxa differed in their respective preferences for substrate and substrate moisture. Members of N. piperi were only on open, moist, sandy flats between rocky areas; those of N. acuta acuta were only on stones; those of N. mannerheimii were active on dry sand and silt at distances up to 10m from the stream margin; and those of N. sahlbergii sahlbergii were on various substrates within two meters of the water margin.

Additional data on nocturnal substrate preferences are critically needed. Meager data presented above are sufficient to suggest that members of different taxa may utilize slightly different microhabitats at night, a fact not apparent from daytime collecting and observations. Night collecting can provide more pertinent data as well as more interesting encounters with these beetles (i.e. during their periods of activity) than daytime collecting.

Summary: microhabitat preferences, distribution and temperature

Geographical and habitat distribution patterns of taxa result from a complex interplay of environmental and historical factors with the

Table 12. Summary of data on nocturnal activity in members of Nearctic *Nebria* taxa.

Name of taxon	(1) Date[1]	(2) Time[2]	(3) Lunar phase[3]	(4) Substrate[4] (A) clay	(B) silt	(C) sand	(D) gravel	(E) boulders	(F) snow, ice
l. lacustris[5]	7/15-8/9	19:00-01:00	?				X		
c. crassicornis	8/11	21:30-23:30	NM						X
c. intermedia[6]	6/31-8/8	02:00	LQ-FQ						X
gyllenhali castanipes[6]	8/17-8/28	03:30	NM				X		X
a. acuta	8/1-8/30	dusk-23:30	FM-NM					X^d	X
s. sahlbergii	8/6-8/9	22:00-23:15	NM		X^m	X^m	X^m	X	
obliqua	6/11-7/23	23:30-01:00	FM				X^m		
pallipes[5]	7/15-8/9	19:00-01:00	?				X		
mannerheimii	8/6-8/9	22:00-23:15	NM		X^d	X^d			
desolata	6/21	22:00-23:00	NM			X^m			

Table 12. (continued)

Name of taxon	(1)	(2)	(3)	(4) (A)	(B)	(C)	(D)	(E)	(F)
eschscholtzii	5/10-11/7	23:00	FM			X^m		X	
g. gebleri[6]	8/28	03:30	NM						X
g. cascadensis	8/9	22:00-23:15	NM			X^m			
m. meanyi	8/3-8/29	20:15-23:30	FM-LQ						X
metallica	8/9	22:00-23:15	NM		X^m	X^m			
v. vandykei	8/5-8/10	dusk-23:30	LQ-NM						X
v. wyeast	8/3-8/30	20:15-23:30	FM-LQ						X
piperi	8/1-8/6	20:15-23:30	LQ-NM			X^m			
purpurata	6/11	23:30-01:00	FM			X^m	X^m		

[1]Data on date of observation include earliest and latest month/day records.

[2]Data on time of observation include earliest and latest nighttime records.

Table 12. (continued)

[3]Code for lunar phase data is as follows: NM=new moon; FQ=first quarter; FM=full moon; and LQ=last quarter.

[4]Superscript letters for substrate data denote the following: [m]=substrate moist; [d]=substrate dry.

[5]Data from Spence (1974)

[6]Data from Edwards (1975, and personal communication)

intrinsic capacities (tolerance) of their members over time. Explanations based on few environmental factors for such long-term and complex interactions are seldom accurate or sufficient. However, my review of macro- and microhabitat distributions among Nearctic Nebria, as discussed above, leads me to conclude that thermal requirements of members of these taxa are preeminent in limiting habitat distributions. I interpret shifts in apparent microhabitat preferences with altitude, latitude and season as responses to temperature. Preferences for certain microhabitat types and substrate, cover, exposure and moisture characteristics of the environment are actually choices among respective effects on temperature--that is, in each instance, temperature effects appear to be critical. One probable exception is seen in nocturnal substrate preferences, presumably because temperatures at night are generally well within tolerance limits of members of most taxa. By extension, it is reasonable to suggest that these same thermal tolerances are (and have been) important in limiting the geographical ranges of taxa (see Kavanaugh (in press A) and section 4.2 below for further discussion).

The ways in which temperature may be operative in limiting habitat and/or geographical distribution are potentially numerous and, at present, impossible to designate for any Nebria taxon. Relationship between microhabitat distribution and temperature may be relatively simple--dependent, for example, on thermal characteristics of available daytime hiding places. Macrohabitat and geographical distributions are probably related to temperature in complex ways, different for and perhaps unique to members of each taxon. For example, Kavanaugh (in press A) noted that northern and eastern limits to the geographical

range of *N. eschscholtzii* corresponded to certain isotherms for mean monthly minimum in air temperature for January. Because members of this species overwinter most commonly as larvae (presumably a more fragile stage than the adult), cold winter temperatures may well limit distribution. However, any number of other circadian, seasonal or longer-term temperature effects may actually be critical in this example and are undoubtedly so in other instances. Temperature relationships may also be different for each life cycle stage, at least in some taxa. The extent to which critical temperature effects can be recognized for any given *Nebria* taxon is dependent on the quality and completeness of temperature and other environmental data. Lindroth (1963a) demonstrated what can be done with sound climatic data. Unfortunately, such data are generally unavailable at present.

3.232 Life history

Lindroth (1961), in his treatment of the majority of Nearctic *Nebria* taxa, presented data on life histories. Through my field and laboratory studies on these taxa and a review of recent literature, a body of new data can now be integrated with his. The results of my review of this expanded data pool are summarized here. Details on life history for the various taxa are presented with descriptions of taxa (section 3.43).

For convenience, I have divided discussion on life history into two parts: (1) diel (daily) activity cycles, and (2) life cycles and seasonal activity.

3.2321 Diel activity cycles

As noted above, members of apparently all *Nebria* taxa are nocturnal--that is, they are actively moving about (at least "on foot"), feeding, etc. on the surface (out from under cover) only at night. That this activity is strictly nocturnal has been substantiated by field experiments only for members of *N. brevicollis* (Williams, 1959; see also Schiller and Weber, 1975, Thiele, 1969a, and Thiele and Weber, 1968) in western Europe. Instances of diurnal or crepuscular activity in one or a few individuals of certain taxa have been noted. Allen (1967) collected two individuals of *N. ingens riversi* Van Dyke seen running on snowfields at midday on the slopes of Mt. Lyell (at 3510m), Sierra Nevada (California). I found one *N. suturalis* individual active on the rocky summit of Grays Peak (4350m) (Colorado) during a heavy, dense mist at about 14:00 hours. I have repeatedly observed a few members each of *N. acuta acuta*, *N. piperi* and *N. vandykei* leaving cover just before sunset at various localities. In spite of these few exceptions, an assumption of strict nocturnal activity is probably valid for members of all Nearctic taxa. Nothing is known, however, about the activity of members of populations living in far northern areas where daylight is continuous during summer months. [See section 3.233 for discussion of flight activity, which, when present, may be strictly diurnal!]

Observations on the nocturnal activity of Nearctic *Nebria* are few. Edwards (1975) has found members of several different taxa active on snowfields at night (Glacier National Park, Montana). Data now available are presented in Table 12 (see also the discussion above on

nocturnal substrate preferences). Times listed represent collecting periods or times of capture of specimens; and, therefore, these data are insufficient for defining actual temporal ranges of activity. Williams (1959) used time-sorting pitfall traps to study activity period in _N. brevicollis_. He showed that activity of adults was restricted to the period between sunset and sunrise; but his sampling intervals were too long to permit more detailed analysis of activity during the night (e.g. comparing activity at different hours). At present, details on the temporal range of nocturnal activity are not known for members of any Nearctic _Nebria_ taxon. We also know nothing about the possible effects of such factors as temperature, humidity, precipitation and the lunar cycle on nocturnal activity in these taxa, although we can assume that one or more of these factors must have some effect.

All existing data on Nearctic taxa suggest that larval activity is also strictly nocturnal. Spence and Bell (unpublished manuscript) have confirmed this for larvae of _N. pallipes_ and _N. lacustris lacustris_. However, Williams (1959) found that, in _N. brevicollis_, first and second instar larvae apparently spread their activity period more uniformly over 24 hours, while third instar larvae are similar to adults (i.e. nocturnal). The extent to which this difference between larval instars occurs in Nearctic taxa is unknown.

As discussed above, _Nebria_ individuals spend daylight hours hiding under cover. In general, the beetles are inactive (motionless) during this time unless disturbed. However, I have found individuals feeding or pairs of individuals copulating in these hiding places. I assume that diurnal feeding results when a potential prey blunders into the

beetle in its hiding place, and that diurnal copulation is either a continuation of an encounter of the previous night or the result of an encounter in the hiding place. I see no need to suggest active, diurnal searching by these beetles for either food or mates.

3.2322 Life cycle and seasonal activity

Life cycle

The life cycle of all *Nebria* studied includes egg, larval, pupal and adult stages, with the larval stage comprising three instars, as in most carabids. Timing of the cycle with the seasons varies considerably among taxa; but, in general one year is required for its completion. However, as discussed below, considerable plasticity is evident in both duration and timing of life cycle events in at least some taxa.

Adults.--Individuals are most commonly seen and collected in the adult stage. Regardless of cycle timing, at least some adults of all taxa can be found during any month of the year, provided that snowcover does not preclude collecting. Even in the extreme example of *N. virescens*, adults of which are not found abundantly in any season and are especially rare during summer months, individuals have been collected in all months of the year. Average longevity of adults is unknown for all taxa; but because at least a few adults are present at any given time, some overlap of consecutive generations must be routine. The extent to which adults are reproductively active for additional years is also unknown. However, Joyce Bell (personal communication) recaptured one *N. pallipes* female in September, 1970, which she had

marked and released one year before. This female laid one egg before dying, and, on autopsy, was found to contain "15 mature eggs and clusters of immature ones." It is probable, therefore, that at least some adults of this and other species live and are reproductively active for more than a single year.

Eggs.--I have not yet found eggs of Nebria in the field. Under laboratory conditions, eggs were, in most instances, deposited in the substrate, singly or in loose clusters. Among those taxa kept in culture, females of N. hudsonica were unique in depositing their eggs in very tight clusters of two to four eggs each. Depth of oviposition is apparently dependent on substrate. In most instances, cultures were maintained on moist peat moss, and eggs were deposited as deep as one centimeter below the surface in this medium. Occasionally, eggs were deposited on the surface. Without exception, these eggs proved to be inviable. One particular group of N. lacustris lacustris females collected on 13 June 1973 at Port-au-Saumon, Quebec, and kept alive in culture deposited eggs on the substrate surface on 23 June. None of these eggs developed further. These same females deposited more eggs beginning on 20 August 1973, a date within the oviposition period for members of this taxon in the field (Spence, 1974). All eggs were deposited in the substrate and numerous larvae eventually emerged. Females may rid themselves of inviable or unfertilized eggs by dumping them on the surface, thereby saving the extra energy needed to carry or bury them.

Eggs of all species studied have a very sticky surface film. Even moist substrate sticks tightly to eggs, suggesting that the substance involved is insoluble in water. Such a binding substance would be of

particular importance for riparian beetles (e.g. most Nebria), because without some holdfast capability, eggs, which float, would be washed from the substrate quite easily.

No data on fecundity or duration of the egg stage are available for members of Nearctic taxa. Penney (1966) reported that females of N. brevicollis, kept in an outdoor insectary (at Rossdhu, Scotland) laid an average of 31 eggs each over an average oviposition period of 27 days. Most eggs required 17 days to hatch. Luff (1976) found roughly equivalent fecundity in N. brevicollis females at Close House (Heddon on the Wall, Northumberland, England) but a much longer oviposition period (lasting from October, 1965 to April, 1966). In my own studies, rate of development was clearly affected by temperature. All cultures were kept at a constant 18°C, a temperature well below daytime temperatures in the field. Development in the laboratory was much slower than in the field for members of most taxa.

Preliminary comparative study of chorionic structure, using a scanning electron microscope (S.E.M.), indicates that eggs of different taxa may exhibit very great surface differences. I plan to explore use of this and other egg characters in a future study.

Larvae.--Nebria larvae have been infrequently collected or studied, probably because they are relatively inconspicuous and because their occurrence is, in general, quite seasonal compared to that of adults. However, during the peak larval period for a particular taxon, larvae are very abundant and easy to collect and observe.

The main obstacle to comparative natural history studies on larvae is (and has been) inability to distinguish larvae of different taxa.

Larvae of N. pallipes and N. lacustris lacustris are the only ones yet described (Spence, Bell and Bell, 1976) among Nearctic taxa. Andersen (1970) redescribed the larvae of N. nivalis nivalis (Holarctic range) and N. gyllenhali gyllenhali (Palaearctic subspecies) from localities in Norway. I plan to develop a key to larvae of Nearctic taxa as part of a future study on the immature stages of Nebria.

Larvae are extremely voracious predators, especially as first instars (see also Penney, 1966:511). Those of all taxa studied in culture were found to be highly cannibalistic, even when other acceptable food was available. They appear to react positively to movement, attacking any small, moving prey (including other conspecific larvae) which pass nearby. In many of these encounters between larvae, however, both participants attack simultaneously and then withdraw from the fray.

I doubt that cannibalism is restricted to laboratory conditions, and, in fact, have occasionally found larvae feeding on other Nebria larvae in the field. It is therefore possible that, in those instances when other prey are scarce, conspecific prey may be an important food source. However, selection for behavior which reduces the incidence of cannibalism should be strong. One possible behavioral adaptation would be adoption of sedentary habits, thereby decreasing or eliminating encounters between larvae. I have repeatedly observed, both in cultures and in the field, that larvae of some taxa (e.g. N. gyllenhali castanipes and N. diversa) construct cells under cover, even as second instar larvae. Some cells, especially those of some third instar larvae, are undoubtedly for pupation and/or overwintering; and larvae in these cells are, in most instances, inactive after the cell is

completed. However, these functions cannot account for all instances of cell construction. Cells in which N. diversa second and third instar larvae were found on 28 October 1972 (Chesterman Beach, Vancouver Island) are illustrated in Fig. 360 . Each cell included a broad, shallow upper chamber and a narrow, deep lower chamber. Larvae in the cells were quite active, frequently found with forebody in the upper chamber and abdomen in the lower. When disturbed, they retreated backward into the lower chamber, much like cicindeline larvae. I suggest that prey are seized as they take cover in the upper chamber, and that forays on the surface are seldom made by or are necessary for these larvae. Encounters with other N. diversa larvae would, therefore, be few. Larvae of many taxa are, however, active on the surface (i.e. they are frequently collected in pitfall traps), as was shown by Luff (1976), Penney (1966) and Williams (1959) for N. brevicollis larvae and by Spence (1974) for N. pallipes and N. lacustris lacustris larvae. Mechanisms for reduction of cannibalism among members of these taxa are unknown. Greenslade's (1964a) pitfall data for N. brevicollis suggest that larval activity is considerably less than adult activity, although, logically, larvae must be more abundant at some time than adults. This finding could be interpreted as evidence for some level of sedentary habits even among species with relatively active larvae.

Rates of larval development in Nebria are, within limits, temperature-dependent (Luff, 1976), and, therefore, vary from year to year and between different localities. Developmental rates have not been studied in Nearctic taxa. Penney (1966) reported that N. brevicollis larvae spent 11 to 14 days in the first instar, 11 to 14

days in the second instar, and a highly varied period in the third (overwintering) instar at ambient temperatures in an outdoor insectary (Rossdhu). Luff (1976) reported that mean development times for the same instars in _N. brevicollis_ members kept at 10°C in an incubator were approximately 23, 27 and 83 days, respectively. As noted above for eggs, laboratory conditions appear to retard larval development, probably because higher field temperatures promote more rapid development there.

Pupae.--In more than eight years of collecting, I have found only six _Nebria_ pupae in the field, including two not yet identified and one each of the following taxa: _N. crassicornis crassicornis_ Van Dyke (15 August 1972, Mount Rainier, Washington), _N. fragilis teewinot_ n. ssp. (13 July 1972, Green Rivers Lakes, Wyoming), _N. gyllenhali castanipes_ (11 June 1973, Mount Albert, Quebec) and _N. obliqua_ (3 April 1973, Edmonton, Alberta). That pupae are so rarely seen suggests that some peculiar microhabitat shift precedes pupation. However, all pupae found were under cover in areas where adults and larvae of the same taxa are commonly collected. Several pre-pupal third instar larvae, representing various taxa, have also been collected in areas commonly occupied by individuals at adult and larval stages. All pupae and pre-pupal larvae were found in relatively large cells (diameter, 1.5 to 2.0cm); and although digging capabilities of _Nebria_ larvae are probably not great, some capacity for excavation is apparent. Pupation may, therefore, generally occur deeper in the substrate than my few discoveries suggest (see also Penney, 1966:507).

Several days prior to the pupal molt (e.g. three days in members

of _N. brevicollis_; Penney, 1966), third instar larvae enter a quiescent pre-pupal stage. Following molt, pupae assume a supine position, supported above the substrate by long, erect setae on the dorsum, just as in other carabids studied (e.g. see Erwin, 1967). At least in members of _N. brevicollis_, duration of the pupal stage is also temperature-dependent (Luff, 1976). In laboratory experiments, pupal period ranged from seven days (at 22°C) to more than 40 days (at 5°C). Penney (1966) reported that eight days were spent in the pupal stage under field conditions at Rossdhu in 1963 and 1964 (Penney, 1966).

Adults of some taxa apparently remain in their pupal cells for a considerable time following eclosion (imaginal molt). Darlington (Lindroth, 1961:74) noted that, in members of _N. suturalis_ on Mount Washington (New Hampshire), eclosion occurs in autumn, but adults remain in pupal cells until spring. I found fully-sclerotized and pigmented adults of _N. piute_ Erwin and Ball in pupal cells on Circleville Mountain (Utah) in June, 1973. Teneral _N. piute_ adults have been collected in September, unassociated with pupal cells (T. L. Erwin, personal communication), suggesting that members overwinter as adults but do not necessarily remain in pupal cells until spring. As teneral adults, _Nebria_ are soft, easily injured and, as observed in both the field and laboratory, subject to predation by fully-sclerotized conspecific adults or other predators. Because mature adults rarely attack one another, a tendency to remain in pupal cells at least through the teneral phase could increase survival and reduce cannibalism among adults.

Life cycle timing

Variation in seasonal timing of the life cycle among carabids has been studied by Greenslade (1965), Larsson (1939), Lindroth (1949) and Thiele (1971). These authors discussed timing of life cycles in relation to geography and synoptic climate, and to geographical and habitat distributions of taxa. They classified beetles according to temporal characteristics of their respective life cycles. Larsson noted that carabids could be described as either "spring breeders" or "autumn breeders," terms also used by Thiele. Lindroth, followed by Greenslade, classified carabids according to stage in which they overwinter--that is, either as "larval overwintering" or "adult overwintering" beetles. These two classification schemes are essentially equivalent. However, as discussed below (section 4.22), stage of overwintering may be important in limiting distributions of taxa and is, therefore, the more significant character.

As outlined by Greenslade (1965), timing of life cycles for taxa in which members overwinter as adults is as follows: breeding, oviposition and larval hatching in spring or early summer; pupation in late summer or early autumn; eclosion in autumn (Fig. 361). On this regime, adults of some taxa may enter a cold (winter) diapause. For taxa in which members overwinter as larvae, timing is as follows: pupation in spring; eclosion in spring or early summer; oviposition and larval hatching in late summer or autumn; larval development in autumn and winter. Adults of some taxa (e.g. _N. brevicollis_) on this regime enter a summer diapause while those of other taxa are active throughout the summer. Overwintering larvae of some taxa (e.g.

N. diversa) remain active until the pre-pupal phase, but those of other taxa may enter a cold diapause (see below).

Life cycle timing in N. brevicollis has been studied in great detail, through both field studies (Gilbert, 1958; Greenslade, 1964a and 1965; Penney, 1966; Richards, 1946; Schiller and Weber, 1975; and Williams, 1959) and laboratory experiments (Luff, 1976; Penney, 1969; and Thiele, 1969b). As noted above, most members of this species overwinter as larvae, and most adults enter a summer diapause (aestivation). Spence (1974) and Spence and Bell (unpublished manuscript) have shown that most members of both N. pallipes and N. lacustris lacustris in Vermont also overwinter as larvae, but that adults there do not enter a summer diapause. Except for Spence's study and brief statements on life history provided by Lindroth (1961), no synthesis of information on life cycle timing in Nearctic taxa has appeared. Table 13 provides a survey of temporal data on life history of Nearctic Nebria. Sources of data used in the table include field collections and observations, laboratory observations from rearing studies, museum specimens and literature records. Museum specimens were principally useful in estimating temporal distributions of adults, especially teneral adults. Statements on life cycle timing in discussions below represent interpretations of data surveyed in the table and presented in more detail with the descriptions of taxa (section 3.43).

Members of 34 (50%) of the 68 Nearctic taxa recognized apparently overwinter almost exclusively as adults. In 11 other taxa (16%), a majority of members overwinter as adults, but some members overwinter as larvae. Members of 10 taxa (15% of the fauna) overwinter almost

Table 13. Summary of data[1] on life cycle timing in Nearctic *Nebria* taxa.

Name of taxon	(1) Adults (A) hardened	(1) Adults (B) teneral	(2) Eggs[2,3]	(3) Larvae (A) first instar	(3) Larvae (B) second instar	(3) Larvae (C) third instar	(4) Pupae	(5) Overwintering stage[4]
virescens	2-12	4-6	<u>11</u>-<u>12</u>	<u>12</u>-<u>1</u>	1	2	?	L[a]
paradisi	6-9	6-8	8	<u>9</u>	<u>10</u>	8	8	A[b]
gouleti	4-10	4-7	<u>8</u>	<u>9</u>-<u>10</u>	<u>9</u>-<u>10</u>	<u>10</u>	?	L
hudsonica	4-10	[5-8][5]	7-8	?	?	<u>9</u>	?	[A/L]
l. lacustris	4-11	[4-8]	<u>6</u>[i]-<u>8</u>	<u>9</u>-<u>10</u>	<u>9</u>-<u>10</u>	9-12	?	[L/A]
l. bellorum	5-10	5-6	<u>8</u>	<u>9</u>	<u>9</u>	<u>10</u>	?	L
n. nivalis	6-9	7-9	7	<u>7</u>	<u>8</u>	<u>8</u>	?	[L/A]
n. gaspesiana	6-7	7	<u>6</u>	<u>6</u>	<u>7</u>	?	?	A

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
c. crassicornis	5–9	7–9	8	8	9	8	8	A[b]
c. intermedia	5–10	5–9	6–7	7–8	7–9	5–10	?	L[a]
gyllenhali castanipes	4–10	[4–8]	6–8	6–10	8	6	6	[L/A]
g. lassenensis	8–10	7–8	?	?	?	?	?	A
g. lindrothi	6–9	6–8	?	?	?	11	?	A
frigida	6–9	6–8	7	7	8	8	?	A
lyelli	7–9	9	?	?	?	?	?	A
a. acuta	5–9	6–8	8	8	10	10	?	A[b]
a. quileute	5–8	7	?	?	?	?	?	A
s. sahlbergii	4–10	[5–10]	8–10	9–11	10–11	10–2	?	L
s. modoc	5–6	6	?	?	?	?	?	L
s. triad	6–8	6–7	?	?	?	?	?	L

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
gregaria	5–9	5–8	$\underline{7}$	$\underline{9}$–$\underline{10}$	$\underline{10}$	$\underline{10}$	?	L
charlottae	?	?	?	?	?	?	?	?
a. arkansana	6–9	6–9	$\underline{9}$	?	$\underline{10}$	$\underline{11}$	7	A[b]
a. edwardsi	5–9	[7–9]	7–8	?	?	?	?	[A/L]
a. oowah	8	8	$\underline{8}$	$\underline{10}$	$\underline{11}$	?	?	A
a. uinta	8	8	?	?	?	?	?	A
f. fragilis	6–8	6–8	$\underline{8}$	$\underline{10}$	$\underline{11}$	$\underline{12}$	?	A
f. teewinot	7–8	7–8	?	?	?	?	?	A
z. zioni	5–8	6–7	$\underline{7}$	$\underline{9}$	$\underline{10}$	$\underline{11}$	?	A
z. oasis	6	?	$\underline{9}$	$\underline{10}$	$\underline{11}$	$\underline{1}$	?	A
suturalis	6–9	7–8	[6–9]	$\underline{7}$–$\underline{9}$	$\underline{7}$–$\underline{9}$	$\underline{10}$	?	A[b]
obliqua	4–10	[4–9]	7–$\underline{8}$	$\underline{8}$–$\underline{9}$	$\underline{8}$–$\underline{11}$	$\underline{9}$–$\underline{11}$	5	[L/A]

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
appalachia	5–9	[5–8]	8	9	9–10	?	?	[L/A]
pallipes	3–11	[4–10]	8–10	8–10	8–10	10	?	L
darlingtoni	6–9	?	?	?	?	?	?	?
mannerheimii	3–10	4–8	8–9	10	10	10	?	L
desolata	4–7	6	8	9	10	10	?	A[b]
navajo	6	6	?	?	?	?	?	?
eschscholtzii	1–12	2–8	8–9	10	10	11	?	L
diversa	2–12	4–7	11–12	12	10	10	?	L
g. gebleri	5–9	5–9	7	7–8	9	10	?	A[b]
g. cascadensis	5–10	5–9	7	7–8	9	10	?	A[b]
g. rathvoni	4–9	7–9	7–8	9	9–10	10–11	?	A
g. siskiyouensis	6–8	?	7	7–8	8	?	?	A

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
g. strawberriensis	5	?	?	?	?	?	?	A
carri	7–8	8	?	?	?	?	?	A
k. kincaidi	6–8	7–8	8	9	10	11	?	A
k. balli	5–9	6–9	?	?	?	?	?	A
s. spatulata	7–9	9	8	9	9	11	?	A
s. sierrae	7–9	7–9	?	?	?	?	?	A
ovipennis	5–9	7–9	8	9	10	11	?	A
m. meanyi	6–10	6–9	7	9	10	11	?	A
m. lamarckensis	7–8	8	7	9	9	10	?	A
m. sylvatica	5–8	7–8	?	?	?	?	?	A
metallica	5–9	5–9	7–8	9	9	10	?	A/L
i. ingens	7–9	7–9	7–8	9	10	?	?	A

Table 13. (continued)

Name of taxon	(1) (A)	(1) (B)	(2)	(3) (A)	(3) (B)	(3) (C)	(4)	(5)
i. riversi	7–8	?	?	?	?	?	?	A
v. vandykei	7–8	8	8	8	9	10	?	A
v. wyeast	6–8	7–8	?	?	?	?	?	A
piperi	5–9	6–9	7	9	10	11	?	A[b]
s. schwarzi	6–9	7–8	7	7	8	8	?	A
s. beverlianna	7–8	8	8	8	9–10	10	?	A[b]
purpurata	6–9	6–9	6–8	8	9	9	?	A
t. trifaria	5–9	7–9	7	9	9	10	?	A
t. catenata	6–9	7–9	?	?	?	?	?	A
t. utahensis	7	7	?	?	?	?	?	A
coloradensis	6–8	7–8	?	?	?	?	?	A
piute	6–9	7–9	7	9	9	9–6	6	A[b]

Table 13. (continued)

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[1]Temporal data presented here are derived from field and laboratory observation, specimen labels, and the literature. Numbers refer to consecutive months of the year (e.g. 1=January).

[2]Data in italics are from laboratory rearing studies alone.

[3]No eggs were collected in the field; but many were obtained as soon as adults were captured. These are considered here as obtained from the field. Superscript "i" denotes eggs which were apparently inviable when deposited.

[4]Assignment of a taxon to one or more classes of overwintering stages is based on review of all available evidence, however meager. Code used for data on overwintering stage is as follows: A =all or almost all individuals overwinter as adults; A^b =most individuals overwinter as adults, but some do so as larvae; L =all or almost all individuals overwinter as larvae; L^a =most individuals overwinter as larvae, but some do so as adults. A/L and L/A =overwintering of individuals in either adult or larval stage, but a few more do so in the first-mentioned stage than in the other.

[5]Brackets denote apparent geographical variation in timing.

exclusively as larvae; and those of another two taxa (three percent) overwinter mainly but not exclusively as larvae. Combining classes, I find that most members of 66% of Nearctic taxa overwinter as adults and those of 18% of the fauna do so mainly as larvae. Variation in overwintering stage among members of N. appalachia, N. obliqua, and six other taxa is too complex to permit assignment of these taxa to one of the above classes at present (see below and species descriptions for further discussion on life cycle timing in these taxa). Overwintering stage is yet unknown for members of N. charlottae, N. darlingtoni, and N. navajo.

An impression obtained from review of the literature on timing of life cycles (see Greenslade, 1965; Larsson, 1939; Lindroth, 1949; and Thiele, 1971) is that individuals of a given taxon are sufficiently synchronous in their development to permit assignment of that taxon to one of the above classes. However, some level of asynchrony appears to be universal in Nebria, in some instances so common that classification of the taxon as a whole is almost impossible (e.g. N obliqua). Luff (1976) reported that some small percentage of N. brevicollis individuals overwinter as adults; and Greenslade (1965) cited evidence for slight geographical variation in adult activity periods in the same species. Evidence for at least slight asynchrony among conspecific individuals is available for all well-sampled Nearctic taxa. Fortunately, general timing patterns are still apparent for most taxa.

I found life cycle timing of some Nearctic taxa surprisingly difficult to characterize, mainly because of interpopulational variation in this character. Variation appears to be correlated, in

one or another taxon, with altitude, latitude, synoptic climate, or with some combination of these factors. For example, at least some members of N. obliqua populations at southern latitudes (e.g. in Colorado; ca. 39°N latitude) overwinter as adults; but members of the same taxon in populations at more northern latitudes (e.g. Edmonton, Alberta; ca. 54°N latitude) overwinter almost exclusively as larvae. Also, most members of N. obliqua populations at high altitudes in Colorado overwinter as adults, while populations at lower altitudes in the same area have many members overwintering as larvae. An example of possible correlation between cycle timing and synoptic climate is provided by N. hudsonica. Members of Rocky Mountain populations (i.e. in an area of "continental" climate) overwinter exclusively as adults; but some members of populations on the Columbia Plateau, an area of more "maritime" climate, overwinter as larvae. Possible correlations between cycle timing and these and other distributional factors were discussed by Greenslade (1965) and Lindroth (1949) and are explored further in section 4.22.

Slight differences in timing were frequently observed between members of different conspecific populations. For example, teneral adults of N. eschscholtzii (members of which overwinter as larvae) are found as early as February in coastal parts of northern California, but only later in the spring in the Sierra Nevada. In general, and especially for members of numerous taxa with significant altitudinal and/or latitudinal ranges (e.g. N. obliqua, N. hudsonica, or N. pallipes), activity begins earlier in spring and continues later in autumn in populations at low altitude or latitude than in populations at higher altitude or latitude. Members of populations which differ in

either of these parameters often show slight asynchrony with respect to one another in life cycle timing. Because developmental rates are often temperature-dependent (see above), it is reasonable to suggest that this asynchrony results where different populations are subject to different temperature regimes.

A particularly intriguing example of intraspecific variation in life cycle timing is seen in N. appalachia (see species description for details). From a study of all available material, it appears that individuals have, in past years, overwintered exclusively as adults or as larvae at different localities in the same year or at the same locality in different years. This and other, less-dramatic examples of variation cited above suggest that, in some taxa, significant plasticity in life cycle timing is possible. By recombining numbers of taxa in the overwintering-stage classes used above, I note that 44 Nearctic taxa (65% of the fauna) show little or no plasticity, but that 21 (30.5%) are moderately to very plastic in this character. A potential for flexibility in timing may account, for example, for the large geographical and life zone ranges of N. obliqua and N. gyllenhali castanipes by permitting adaptation of local populations to a variety of local and regional climates. As noted above, the geographical range of N. eschscholtzii, a species with an approximately equivalent life zone range to that of N. obliqua, is nonetheless quite restricted, probably because larval development in members of this species requires activity throughout the winter months.

Nebria living at high altitudes face a unique problem affecting timing of life cycles--namely, the possibility of extreme variation in timing and amount of snowfall, snow accumulation and resultant length

of the snow-free period. For example, members of *N. crassicornis crassicornis*, *N. paradisi* and *N. vandykei vandykei* occupy areas of Paradise Park (Mount Rainier, Washington) which remain completely covered with snow through the summer and autumn in some years. For life in such areas, some level of plasticity in cycle timing would be desirable. In fact, I have found first and third instar larvae, a pupa and adults of *N. crassicornis crassicornis* and mature adults and third instar larvae of *N. paradisi* and *N. vandykei vandykei* all at the same time (early August, 1972) in Paradise Park. In the previous year (1971) snowcover remained intact until late August. It is possible that these examples of asynchrony resulted when development of some individuals was so retarded by unfavorable climatic events that they required more than one year to complete their life cycle. Most members of *N. crassicornis crassicornis* overwinter as adults; but in years when winter snowfall begins early, individuals may be forced to overwinter as larvae. From field observations, it is apparent that this is not always fatal, but rather that *N. crassicornis* larvae can pupate in the spring and 'catch up' with other members of the population before the breeding season is over. Similar findings were obtained under laboratory conditions with *N. piute* individuals. Most members of this species also overwinter as adults. However, development of larvae in culture was slower than in the field, and cultured larvae failed to pupate in autumn. Larvae kept through the winter at 1°C pupated in the following spring, shortly after their transfer to warmer (10°C) conditions. Such plasticity in cycle timing is undoubtedly of significant adaptive value for life at high altitudes.

It follows from the above discussion that, in some instances, striking differences in life cycle timing among members of different conspecific populations may be taxonomically insignificant. Slight asynchrony between members of different populations, especially those at different altitudes or latitudes, is probably even less significant if temporal patterns observed conform to those predicted based on differences in "growing seasons" at different altitudes, latitudes, etc. (see above). Therefore, only the broadest possible temporal characterizations of taxa are generally useful; and assignment of high taxonomic significance to slight interpopulational variation in life cycle timing is not justfied.

Control of life cycle, development and reproduction

Temperature and other environmental factors alone cannot account for the strong developmental synchrony observed in members of 69% of Nearctic taxa, nor even for the limited synchrony seen in members of more 'plastic' species (e.g. N. obliqua). Because members of different sympatric taxa often differ grossly in life cycle timing, some intrinsic (inherited) control mechanism must be operative. No such mechanisms have yet been described for Nearctic taxa, but considerable work has been done on life cycle control in N. brevicollis.

Thiele (1969b) found, through laboratory studies, that cold temperatures (2 to -4°C) are required for larval development during the autumn and winter, and that higher spring temperatures trigger pupation. According to Thiele, summer diapause (aestivation) is dependent on photoperiod. However, Penney (1969) reported that diapause occurred under all photoperiod regimes provided

experimentally, but that starvation of adults prevented it. From results of these and other experiments, Penney concluded that body fat content regulates the onset of diapause. Stimulus for termination of diapause is unknown. Penney's findings exclude change in photoperiod from such a role, but implicate decreased daylength as the stimulus for initiation and completion of ovarian development in females and final maturation of testes in males. This interpretation is supported by studies on the neuro-endocrine complex in N. brevicollis (Ganagarajah, 1965). Increased size and activity of the corpora allata, which presumably mediate gonad maturation, are associated with decreased daylength. Thiele (1969b) suggested that decreased temperature was also required for oöcyte maturation.

Some of these same controls may be operative in Nearctic taxa in which members overwinter as larvae; but for those taxa in which adults overwinter, a different set or sequence of controls is required.

Seasonal activity of individuals

Some activities which are apparently restricted to certain seasonal periods and are, in themselves, of interest include: (1) short-range migrations of members of some taxa to and from streambanks; (2) flight; (3) mating; (4) aestivation; and (5) winter activity. Short-range seasonal migrations in riparian Nebria were discussed above (section 3.231). Flight is considered in a following section on locomotion and dispersal. Only two confirmed flight records for Nearctic Nebria are known, both for males of N. crassicornis intermedia Van Dyke in September, 1974.

<u>Mating</u>.--Little is known about mating behavior in Nearctic <u>Nebria</u>. Kavanaugh and Martinko (1972) reported on a nebriine equivalent of 'honeymoon cruises' for members of <u>N. purpurata</u> in New Mexico. Copulating pairs of these beetles were seen leaving the streambank and swimming on the water surface to emergent rocks in midstream. Other pairs, but not individuals, were found resting in tandem on these rocks. The significance of this behavior remains unknown. Other literature notes on mating include only date records for copulation observed in the field (Larochelle, 1972). I have observed copulating pairs representing many different Nearctic taxa (see Table 13A). Most of these were found hiding under cover during daylight hours. Copulating pairs of <u>N. vandykei</u> (both subspecies) were found resting, running and feeding on snow at night.

In laboratory cultures of several taxa studied, males repeatedly attempted copulation with any available individuals, including other males, in the presence of a female during the mating period. Mating activity in males is, therefore, probably stimulated by a female pheromone in members of these and, perhaps, all <u>Nebria</u> taxa. No data on the source, composition or specificity of the proposed pheromone are available.

Copulation is apparently a prolonged activity, unless the beetles are disturbed. As suggested above, pairs found during the day have probably remained <u>in copulo</u> since the previous night. Duration of the period of mating activity under field conditions is unknown for Nearctic taxa. Studies of <u>N. virescens</u> adults in culture indicate a surprisingly long period. A single pair of adults captured in May,

Table 13A. Data on field and laboratory observations on copulation in Nearctic Nebria.

Taxon	Where?[1]	Month	Time
virescens	H	Oct.-Dec.	-----
frigida	H	July	2:00-18:00
crassicornis intermedia	H	July	-----
n. nivalis	H	July	12:00-20:00[2]
n. gaspesiana	H	June	15:00
gouleti	L	Sept.	-----
l. lacustris	St	July-Sept.[3]	-----
l. bellorum	L	Sept.	-----
paradisi	H	Aug.	12:00-15:00
metallica	H	July	11:00-18:00
schwarzi beverlianna	H	Aug.	16:00
piperi	H	Aug.	16:00
v. vandykei	Sn	Aug.	21:30-23:30
v. wyeast	Sn	Aug.	23:30-01:00
piute	H	June	12:00
t. trifaria	H	Aug.	16:00
i. ingens	H	July	15:00
a. acuta	H	Aug.	10:00-18:00
a. arkansana	H	Aug.	10:00-15:00
a. edwardsi	H	July-Aug.	11:00-19:00
f. fragilis	H	Aug.	16:00
f. teewinot	H	Aug.	18:00

Table 13A. (continued)

Taxon	Where?[1]	Month	Time
gregaria	H	July	14:00-19:00
s. sahlbergii	H	July-Sept.	14:00
eschscholtzii	H	Sept.-Oct.	16:00
diversa	H	Sept.-Oct.	-----
suturalis	H	June-July	14:00
pallipes	St	Aug.-Oct.[3]	-----

[1] Code used to denote microhabitat in which copulating specimens were found is as follows: H = hiding under stones, logs, or other cover; L = in laborartory rearing containers; Sn = on surface of snowfield or glacier; St = on open streambank, not under cover.

[2] Data from Larochelle (1972).

[3] Data from Spence (1974).

1971 were first observed in copulo in late September. From that time until late November, 1971, the beetles were found copulating every time their cage was examined. Eggs were first found in mid-November. Mating activity periods for members of all other taxa kept in culture were shorter, in most instances lasting only a few weeks.

Aestivation.--Although aestivation (summer diapause) is well-documented for members of N. brevicollis (see above), it is yet unknown among members of the Nearctic fauna. Very few specimens of N. virescens have been collected during summer months; and life cycle timing among members of this species is similar to that for N. brevicollis members. However, present data are insufficient to support a summer diapause in adults of N. virescens. Aestivation is most unlikely in members of all other Nearctic taxa, based on collection records for adults.

Penney (1969) reviewed previous suggestions on the possible significance of aestivation in N. brevicollis and concluded that it served as a means to avoid energy waste during periods of low food supply. Hågvar and Østbye (1974) have shown that respiration rate (and, therefore, consumption of food reserves) increases significantly with activity in members of N. gyllenhali and N. nivalis. Greenslade's (1965) suggestion that aestivation helps to synchronize breeding and/or delay it until a more favorable period for larval development is also supported by available data. Gilbert's (1958) contention that diapause facilitates gonad maturation, and Tipton's (1960) suggestion that it permits adults to avoid unfavorable periods of low humidity and/or high temperature are contraindicated (Penney, 1969).

Winter activity.--Some of the more intriguing questions about Nebria life history which are yet unanswered concern their activities in winter. Members of taxa which occupy areas at high latitude or altitude must endure winter conditions for more than half of the year. An understanding of the means by which these beetles survive, even thrive, at present is critical for understanding their evolutionary history, at least since pre-Glacial time.

Members of Nearctic taxa which occupy areas with mild winter climate are apparently active through the winter. For example, overwintering larvae of N. eschscholtzii, N. diversa and N. virescens remain active and continue development during winter months. A few active adults of N. eschscholtzii and N. virescens have also been found in winter. However, little is known about the winter activity of Nebria in areas covered by snow. Are these beetles active on the snow surface in winter? Are some active under the snow cover? Do members of some species become inactive, enter a 'cold diapause,' in winter? Is there a significant increase in mortality during this period? None of these questions can be answered at present because virtually no field studies on Nebria have been made in winter.

Overall cold-tolerance in members of Nebria taxa inhabiting high altitude and latitude areas is demonstrated by their ability to remain active on and in the vicinity of snow and ice during summer months. Some level of cold-tolerance in winter can reasonably be assumed. Østbye and Sömme (1972) observed some freezing tolerance, at least at temperatures above -10°C, in members of another nebriine taxon, Pelophila borealis Paykull. As noted by these authors, microclimate in

sub-nival air-spaces is often milder than above the snowcover, due to insulative properties of the latter. Temperatures under the snowcover are often quite stable, and, even in high altitude areas, may rarely drop below freezing (0°C). Conditions under the snow, therefore, may be favorable for activity of Nebria in winter; but whether or not the beetles are, in fact, active under the snow is unknown. Activity on the snow surface is less likely, except during unseasonally warm periods. The only available field evidence for winter activity among Nearctic Nebria in cold climate is that gathered by John Spence (personal communication) for larvae of N. pallipes and N. lacustris lacustris in Vermont. He collected numerous larvae of these two taxa in pitfall traps after the first winter snowfall and until the traps became deeply buried in snow and, therefore, ceased to function. Unfortunately, he was unable to determine how long this activity persisted because of extreme difficulty in sampling during winter.

3.233 Other aspects of natural history

In this section, I discuss present knowledge of Nebria populations and of the role of these beetles in food chains.

3.2331 Studies on Nebria populations

To date, there have been no studies to determine the size, density, dispersion or sex ratio of Nearctic Nebria populations. Population studies among nebriines have been confined to N. brevicollis in Europe.

Population size.--Greenslade (1964a) used the mark-release-recapture

method (Bailey, 1952) to estimate the size of a population of *N. brevicollis* in an isolated beech litter plot at Silwood Park (Berkshire, England). His estimates of population size (total number of adults present) during October, 1959 (maximum of 2300 individuals) and October, 1960 (maximum of 200 individuals) differ significantly. He suggested that population size may vary greatly from year to year, with fluctuations dependent on one or more climatic factor(s) (but see below for an alternative interpretation). Changes in population size undoubtedly occur in Nearctic *Nebria* also. Whether or not Greenslade was actually studying a *population* as defined by Mayr (1969) is unclear. Most *Nebria* populations are, however, more broadly extended in space; and their size would therefore be more difficult to estimate.

Population density, dispersion and aggregation.--Density (i.e. number of individuals per unit area) is more easily estimated than size, again using mark-release-recapture techniques. Penney (1966) estimated that density of new-generation *N. brevicollis* adults at Rossdhu during June, 1962 was 0.945 individuals/m^2. In June, 1963 and 1964, estimated densities were 0.827 and 0.570 individuals/m^2, respectively. Both Penney and Greenslade (1964a) found that dispersion (spatial distribution of individuals) in *N. brevicollis* populations was non-uniform. As shown by their studies, and in general, individuals tend to be found more commonly in some areas than in others(see above for discussion of microhabitat distribution). For example, I estimated (by hand collecting during daylight hours) that density of *N. eschscholtzii* adults along a three meter long section of stream bank (Salt Creek, near Oakridge, Oregon) was 83 individuals/m^2 in areas

within one meter of the stream edge, but less than one individual/m^2 in all areas at greater distances from the water.

Similar responses of several individuals to environmental gradients in selecting preferred microhabitats may alone account for many instances of clustering. However, at least in some instances, positive response to the presence of other individuals also leads to aggregation. Greenslade (1963a) determined experimentally with _N. brevicollis_ adults that (1) individuals aggregate, even in a microclimatically uniform area; (2) male locomotory activity is apparently reduced in the presence of females; and (3) crowding appears to inhibit locomotory activity in both sexes. Penney (1969) observed that aggregation often preceded diapause; and I have found unusual aggregations of active _N. eschscholtzii_ and _N. arkansana arkansana_ Casey adults (see below, section 3.43, for details). Greenslade (1963a) suggested several possible advantages obtained from aggregation (see also Kavanaugh, 1977); but its significance in _N. brevicollis_ and in Nearctic _Nebria_ is yet unknown.

Sex ratio.--No data are available on sex ratio for populations of Nearctic _Nebria_. Some large samples (over 200 adults) I have collected, representing several different taxa, were found to contain, mainly or exclusively, either males or females. The significance of these few random samples is unclear; but they may indicate that, at least for brief periods, sex ratios may depart radically from unity (i.e. from a 1:1 ratio). Greenslade (1964a) found approximately equal numbers of _N. brevicollis_ males and females in the population studied at Silwood Park.

In most instances, I have found the spatial distribution of males and females coincident in Nebria populations. However, at Dutch Harbor, Unalaska Island (Aleutian Islands, Alaska), in July, 1973, males and females of N. gregaria appeared to favor adjacent, but slightly different microhabitats (see species description for details). The significance of this observation is unknown.

3.2332 Trophic relations

In this section, I review what is presently known about trophic relations of Nebria with other biotic components of their environment. Notes from the literature are augmented by my field observations in brief discussions on Nebria feeding and food, and on their predators and parasites.

Feeding and food

Nebria individuals are predators (Evans, 1965a; Lindroth, 1961; and Spence, 1974), feeding on a wide variety of arthropodan and other invertebrate prey. As noted above, larvae are extremely voracious predators and are often cannibalistic (at least in culture). Adults rarely attack hard-bodied prey or each other (except for teneral adults; see above). My field and laboratory observations on members of several taxa suggest, however, that Nebria are also facultative scavengers. Adults of all species kept in culture readily accepted dead arthropods or ground beef as food. Beetles foraging at night on snowfields (e.g. N. vandykei adults) often eat dead and/or frozen arthropods. Feeding is generally associated with nocturnal locomotory activity; but, as noted above, some individuals are found eating in

daytime under cover.

Evans (1965a, 1965b and 1965c) has studied the feeding method of N. brevicollis adults. Sharp, powerful mandibles cut through the prey's body wall and chop it into small pieces. Maxillae rake the bulk food toward the oral cavity, where it is forced down ("bolted") through the esophagus to the crop. The proventriculus grinds food to a smaller size and controls its flow to the midgut. Evans claimed that no external digestion occurs in feeding of N. brevicollis adults; but my laboratory observations on Nearctic Nebria adults and the liquified remains of large prey after feeding suggest otherwise. All other aspects of feeding in Nearctic Nebria appear to agree with Evans' findings.

Because exoskeletal fragments of prey are consumed by Nebria in feeding, analysis of crop contents can help to identify some of the prey taken. This technique was used by Davies (1953 and 1959) and by Penney (1966) in studies of prey preferences of N. brevicollis adults and by Spence (1974) in similar studies on N. pallipes and N. lacustris lacustris adults. Both Davies and Penney reported that collembolans were the preferred prey of N. brevicollis adults, with dipterans, mites, other assorted insects, spiders and earthworms (in that order) less commonly consumed. Spence reported similar prey in similar relative numbers in the apparent diets of both N. pallipes and N. lacustris lacustris adults, the latter favoring collembolans more markedly than the former.

Penney (1966) noted that range in prey size for N. brevicollis adults, as indicated by analysis of crop fragments, was from 0.5 to 4.0 mm. Spence's data also suggest that small-sized prey are

preferred. However, I have repeatedly observed adults of several Nearctic species feeding on large, soft-bodied prey. For example, I have found adults of several taxa (e.g. N. eschscholtzii) eating live stonefly (Plecoptera) adults. One third instar larva of N. gebleri gebleri was found eating a caddisfly (Trichoptera) adult much larger than itself. Adults of N. vandykei will apparently feed on any invertebrate they find on snowfields at night (e.g. large coccinelid adults (genus Anatis), moths, dipterans, and even other (immobilized) carabids). I suggest that crop fragment analysis, although useful, is biased in favor of small-sized prey. Because there must be some limit to the maximum fragment size consumable, and because identifiability of fragments decreases with a decrease in their relative size, recognizable fragments of small prey will be better represented in the crop. Also, Nebria adults (observed in culture) feed discriminately on larger prey, consuming soft, internal parts and avoiding the body wall once it has been opened. Smaller prey can be consumed almost whole. An opportunistic feeding strategy is, therefore, probable for most or all Nearctic Nebria. Small to large and both dead and live invertebrates can be eaten; but diet in a particular instance is dependent on prey availability.

Predators and parasites

Predators.--Little is known about actual predators of Nearctic Nebria. However, because these beetles are often quite abundant, especially in riparian habitats, a variety of nocturnal insectivores could feed on them routinely. Amphibians are likely predator candidates in streamside habitats. R. T. Bell (personal communication) found 13

N. lacustris lacustris adults in the stomach of one toad (Bufo americanus Holbrook) in Vermont; and Larochelle (1976b) found adults of N. gyllenhali castanipes in a toad (same species) in Quebec.

Pratt and Hatch (1938) found remains of N. virescens adults in nests of Black Widow spiders (Latrodectus mactans Fabricius) on Whidby Island (Washington). Spiders are also common predators in riparian and alpine habitats; but none have yet been recorded as preying specifically on Nebria in these areas.

In montane areas, insects flying at low altitudes are often caught by upslope winds and eventually dropped over cold snow and ice areas at high altitude. Unable to fly or even walk at such cold temperatures, they remain stranded there. I have frequently seen birds (identity unknown) eating these insects and other arthropods on the snow surface during the day. In some areas, adults of several Nebria species also forage on these stranded prey, but at night. Nocturnal activity in these beetles may, therefore, aid in avoidance of avian predators. I have not observed potential predators of Nebria active on snowfields at night.

Parasites.--Few endo- and ectoparasites of Nebria have yet been recorded; but, undoubtedly, many remain to be discovered. Just as with other aspects of Nebria natural history, parasitism has been formally studied only in the Palaearctic N. brevicollis.

Phaenoserphus viator (Haliday) (Hymenoptera: Proctotrupidae) has long been known as an endoparasite of N. brevicollis and other carabid larvae (Critchley, 1973; Davies, 1959; Elliott and Morley, 1907-11; Luff, 1976; and Richards, 1946). Luff estimated that 25% mortality in

third instar N. brevicollis larvae was due to parasitism by P. viator and Phaenoserphus pallipes (Latreille) combined in one study area (Silwood Park) in 1966. He noted that, in comparisons among N. brevicollis populations of varied density, mortality due to parasitism appeared to be density-dependent (i.e. relatively heavier parasite infestations in denser beetle populations). He also suggested that these parasites could significantly affect N. brevicollis population size, and, further, that the ten-fold decrease in the Silwood Park population between 1959 and 1960 noted by Greenslade (1964a) could have been due to parasitism rather than adverse climate.

Luff (1976) also found nematode endoparasites (members of Hexamermis sp. and Mesodiplogaster iheritieri (Maupas)) in N. brevicollis larvae.

To date, there have been no published records of parasitism in Nearctic Nebria; but one can now be reported. Two adult gordian worms (Nematomorpha: Gordioidea: Gordius) emerged through the head of one N. sahlbergii sahlbergii Fischer von Waldheim adult collected on Vancouver Island (British Columbia) by Henri Goulet. Visual comparisons of biomass indicate that interior structure of the beetle must have been almost completely replaced by the worms; but the beetle was alive and active when found.

Many adults (both museum specimens and those collected and kept alive), representing many different Nearctic Nebria species, have been found carrying one or more Histiosoma maritimus (Oudemans) (Acarina: Anoetidae) immatures. These mites (Fig. 363) were usually found on the thoracic venter, especially on the prothorax, sometimes clustered in large numbers. Exuviae were also frequently found, still attached

to the venters of some adults. I found no indication that these mites harmed or restricted the activity of their hosts in any way. They are, therefore, probably phoretic rather than ectoparasitic.

3.234 Locomotion and dispersal

My main purpose in presenting data about these topics is to provide a context for evaluation of various zoogeographic hypotheses (section 4.2). Limits to locomotory powers of individuals necessarily place certain constraints on their dispersal and, ultimately, on distributions of their respective taxa. Understanding of distributional shifts or of past, present or potential barriers to dispersal (and distribution) requires at least rudimentary knowledge of locomotory and dispersive capabilities of taxon members.

3.2341 Locomotion

Locomotion (i.e. moving by one's own power) in Nearctic _Nebria_ can be divided into terrestrial (walking and running), aquatic (swimming and walking underwater) and aerial (flight) components. Each of these locomotory modes is discussed separately below. The terrestrial mode is used routinely by members of all Nearctic taxa, the aerial and aquatic modes used to an unknown degree and by members of only some taxa.

Terrestrial locomotion (ambulation)

Evans (1977) recently reviewed ambulation among Adephaga. Using his classification of locomotory types, _Nebria_ can be described as "fast runners/ poor wedgepushers." As suggested by this description, these beetles are capable of relatively rapid movement; but their

delicate stature and long, slender legs provide little pushing power.

As noted above, most ambulatory activity is nocturnal. Beetles observed in the field appear to run rapidly only when disturbed. Normal and maximum gait speeds of various species have not yet been studied experimentally. My crude laboratory estimates of running speeds for members of _N. hudsonica_ and _N. gyllenhali castanipes_ (at 18°C) were, respectively, 55 to 95 mm/sec and 85 to 125 mm/sec. Repeated field observations on disturbed members of single taxa at different temperatures indicate that, within limits, speed increases with temperature. However, as noted above, members of some taxa (e.g. _N. vandykei_) can run rapidly even at very low (at or near 0°C) temperatures (e.g. on snow or ice at night). I cannot yet suggest a relationship between size and speed (see Evans, 1977), although this could be tested experimentally.

Interspecific differences in speed and other gait characteristics are observable in the field. For example, members of _N. darlingtoni_ and _N. gebleri rathvoni_, when found together, are distinguished by differences in running stance, although they are otherwise similar in appearance. The former run rapidly with a very low, wide stance, whereas the latter are slightly slower, with an elevated, narrower running stance. In contrast to the swift, agile members of most Nearctic taxa, _N. suturalis_ members run with a clumsy, lurching gait, very similar to that of _Diplous_ (Patrobini) adults. They are, therefore, readily separable in the field from similarly-colored _N. gyllenhali lindrothi_ adults, with which they share alpine talus slopes (Front Range, Colorado).

Although my data are yet too incomplete to evaluate properly, gait characters among Nearctic Nebria may prove to be taxonomically useful, especially for field recognition and discrimination. Unfortunately, these traits appear to be relatively plastic, probably evolve rapidly, and would, therefore, be of little use in demonstrating phylogenetic relationships.

Little is known about ambulatory ranges of Nebria adults. I have found N. vandykei adults on snowfields as far as 100 m from nearest bare rock or soil less than two hours after dusk (when these beetles normally become active). At this pace [average about 14 mm/sec], they could easily cover a linear distance of 400 m in one night; and because they are capable of much faster movement, at least in bursts, their range is probably much greater. Edwards (1975) found a N. crassicornis intermedia adult active on a snowfield in daylight "a half mile from nearest rock or soil." Assuming that the beetle walked rather than flew (see below) to the point where found, it covered at least 800 m, probably in less than 24 hours (beginning early the preceding night). An average speed of 10 to 20 mm/sec would satisfy requirements of this estimate. The above examples suggest that snowfield-prowling Nebria may cover surprisingly large distances when active. In contrast, Greenslade (1964a and 1964b) found that, during their seasonal periods of locomotory activity, N. brevicollis adults moved an average of 3.67 m/night when disturbed (i.e. immediately after being marked for study) and 1.98 m/night when undisturbed. These values may be underestimates of distances normally covered per night because, by using pitfall traps with mark-release-recapture studies, beetles could move only until trapped. However, both the nature and extent of preferred habitat may

affect the speed and distance of movement (Greenslade, 1964b). Woodland beetles, such as _N. brevicollis_ members, may encounter more obstacles and more varied terrain than snowfield-prowling beetles and, therefore, move more slowly and cover less ground.

No data on lifetime ambulatory ranges of adults are available. Such information would be useful in considering their dispersal potential (see below).

Aquatic locomotion

Aquatic locomotion is probably restricted to those taxa whose members occupy riparian habitats. While members of all but one species lack obvious structural adaptations for swimming or other movement in water, they are competent surface swimmers. Swimming activity of copulating _N. purpurata_ pairs was noted by Kavanaugh and Martinko (1972; and see above, section 3.2322). Members of several taxa, notably those of _N. zioni_ Van Dyke, _N. meanyi lamarckensis_ n. ssp. and _N. ingens_, commonly avoid capture by hurling themselves into cascading streams. I assume that the beetles are subsequently able to swim to safety and resume normal activity.

Members of _N. ingens_ are unique among Nearctic species in having apparent structural adaptations for locomotion underwater. Unique tarsal shape (Fig. 245) and reduced ventral vestiture (Fig. 242) (see also species description) facilitate walking underwater, over even the upper surfaces of submerged stones (Kavanaugh, manuscript in preparation). Adults are able to walk upstream underwater even against a strong current. Although members of other species may take refuge underwater when disturbed, they quickly float to the surface or are

swept downstream unless they remain wedged under or between submerged stones.

In summary, riparian Nebria do make use of adjacent streams, at least in some instances. All can swim on the stream surface and some also move over submerged substrates. The implications of this capability for both active and passive dispersal in flowing water are discussed below (see section 3.2341).

Aerial locomotion (flight)

Based on present data, flight is evidently an extremely rare event among Nearctic Nebria. I know of only three proven flight records for Nebria members. Lindroth (1945; see also 1961) reported on the "spontaneous flight" of a N. brevicollis adult [sex unknown] on 4 July 1944 [hour unknown] at Grebbestad, Sweden. G. E. Ball and J. Belicek (personal communication) collected adults of N. crassicornis intermedia in flight on two occasions in Alberta [Prospect Creek, 5.3 miles nw. of Mountain Pass on ne. slope of Prospect Mountain (1670m; 21 September 1974, 17:00; 2 males caught flying along the stream margin); and Pembina River, 30 miles se. of Robb (1300m; 22 September 1974, 12:00 to 15:00; 1 male).

Two essential prerequisites for flight are: wings and functional muscles to power them. Of the 42 Nearctic Nebria species, 16 (38%) have apparently all members with full-sized hindwings and 20 (48%) have all members with hindwings reduced in length, width or both. Six species (14%) have some populations in which all members have full wings and others in which all members have reduced wings.

Any reduction in relative wing size undoubtedly renders an individual

incapable of flight; so only those beetles with full-sized hindwings can be considered potential fliers. Lindroth (1961), citing the work of Gislen and Brinck (1950) on Palaearctic N. gyllenhali adults and comments from G. W. Ball (in litt.) on N. metallica adults, suggested that, even in some, if not most, full-winged Nebria, flight muscle may not (or only incompletely) develop, thereby precluding flight. No detailed studies of Nearctic Nebria flight muscle development have yet been made.

Darlington (1936, 1943 and 1971) has demonstrated that, under certain environmental and/or historical conditions, especially in certain habitats (i.e. on islands and mountains), hindwing atrophy has been a frequently and independently repeated transformation among carabid beetles. [Discussions of wing atrophy and associated changes in other structures and of possible selective pressures favoring these changes are presented below, section 4.41]. Because hindwing atrophy is so common, especially among Nebria, I surmise, with Darlington (1936 and 1943) and others, that, in fact, functional hindwings are retained in a lineage through time only at some high 'price,' and that beetles cannot 'afford' wings they do not use, at least occasionally (see below). I therefore assume that, in spite of the paucity of flight records, fully-winged adult Nebria do fly, if only rarely. Data on flight muscle development could be used in testing this assumption, but only if muscle development throughout all of adult life is considered. If, for example, flight in Nebria is only seasonal or climatically opportunistic (see below), flight muscle development may also be seasonal or at least asynchronous with development of other structures (see Carter, 1976, for data on the timing of wing muscle

development in Agonum retractum (LeConte) adults). Muscles may therefore be functional only during a brief part of adult life; and short-term surveys of muscle development might overlook this period completely.

Flight records to date suggest that, although Nebria are normally nocturnal, their flight may be diurnal, perhaps exclusively so. There are no proven nocturnal flight records for Nebria. Edwards (1975) reported on two N. obliqua ("N. obtusa LeConte")adults found "at lights" in Glacier National Park (Montana) on 23 July 1967. However, both were found on the ground; and the lights were located about 30 m from a stream (J. G. Edwards, personal communication). It is therefore unclear whether the beetles walked or flew to the lights. Although a majority of carabids which fly at night are collected at lights, it is still possible that Nebria adults fly at night yet are not attracted to (and therefore not collected at) lights.

Critical minimum body temperatures for flight are undoubtedly universal among flying insects (Chapman, 1969), although intergroup and interspecific differences in threshold temperatures are great. Because Nebria characteristically seek out and occupy cool to cold microhabitats, minimum temperatures for flight may be attained rarely and only in daytime (as suggested by available records). Among Nebria, microhabitat requirements seem to take precedence over flight requirements; and some behavioral shifts may therefore be required for adults to take advantage of their flight capability. A temporary change from nocturnal to diurnal activity may be one such shift, but others may also be involved.

An important question yet unanswered is 'Why do Nebria fly?'. The

flight records for _N. crassicornis intermedia_ (see above) serve to confound rather than clarify. Only three specimens--all males--have been taken in flight. Flights were in late September, when days are shorter and mean maximum daily temperatures much lower than in preceding months. Also, most _N. crassicornis intermedia_ individuals overwinter as larvae; and field data from diverse sources indicate that adults have mated, females have oviposited and larvae have already hatched and developed to second instar stage by September in most years. If the observed events are representative of typical flights by members of this taxon (and they may not be), their significance is unclear. Flight prior to mating could be important for location of mates or in reduction of inbreeding (i.e. among siblings) and maintenance of genetic variability throughout populations. Flight (by females) after mating, but before oviposition, could be important in reduction of crowding and intrapopulational competition through both internal and extralimital dispersal (see below). One possible advantage to flight after the oviposition period would be in exploiting suitable but unoccupied areas (either within or outside the normal range of the population). For this strategy to be effective, however, adults would have to survive, mate and successfully reproduce the following year in the new area. Both males and females would have to disperse, unless females could retain viable sperm for more than a single season. An alternative explanation for flight is that the latter is related to annual runoff cycles and flooding of riparian habitats, purely as an escape mechanism. At present, I have no direct evidence in support of either of these hypotheses (see section 4.41 for

discussion of wing size and flight in relation to habitat and geographical distributions).

3.2342 Dispersal

Udvardy (1969) defines dispersal as "the process whereby an organism is able to spread from its place of origin to another locality." However, embraced by this concept are two classes of events, each of different zoogeographic and evolutionary significance. In the first class are dispersals entirely within the normal range of a population (or a taxon). This type of dispersal is restricted to individuals. It permits outbreeding, gene flow and maintenance of variability throughout populations; and it contributes to the maintenance of geographical distribution by balancing the effects of local extinctions. Platnick (1976) recognized the need for a term to distinguish this type of dispersal and suggested "dispersion" as appropriate. However, as noted by Armstrong (1977), the latter already has a precise (but different) meaning in both ecology and physics (e.g. in gas laws); and its expropriation and redefinition is unjustified. I here use the term internal dispersal for this type of dispersal.

The second type of dispersal, which I term extralimital dispersal, is movement to an area outside the normal range of a population (or taxon). It may refer to the movement of individuals, populations or taxa. Extralimital dispersal of individuals results in at least transient increases in or shifts of the ranges of populations or taxa; and, therefore, these groups can also be said to have undergone extralimital dispersal. The zoogeographic and evolutionary importance of this type of dispersal has long been discussed (see

Darlington, 1957, 1965 and 1971) and is currently under spirited attack by some biogeographers (see Ball, 1976; Croizat, et al., 1974; Nelson, 1975; and Rosen, 1976).

Hypotheses concerning the role of both types of dispersal in the historical development and maintenance of present distributions and distributional patterns among Nearctic Nebria are discussed below (section 4.2). The following discussion summarizes scant available data on both internal and extralimital dispersal and evaluates dispersal potential.

Means of dispersal

Udvardy (1969) noted that "spread or ease of locomotion is in no direct relation to speed or ability of dispersal," and that distributions of taxa and the relative vagility (i.e. the intrinsic ability and tendency to move) of their respective members are not always directly related. For example, taxa (e.g. most birds) with highly vagile members may not occupy ranges as extensive as taxa (e.g. some land snails) in which members have relatively low vagility. Potential relationship between vagility and distribution may be obscured by historical events and because organisms may disperse passively as well as actively. Active (i.e. self-powered) dispersal is, in fact, directly related to locomotory capability; but passive dispersal (i.e. dispersal by means of a carrier) bears no (or perhaps, in practice, some inverse) relationship to locomotory capability. With the discussion above on locomotion as preface, I here attempt to assess the relative and potential importance of different active and passive means of dispersal for Nebria.

Active dispersal.--As noted above, Nebria may use from one to three locomotory modes, including ambulation, natation (including both surface and bottom locomotion) and flight. Each of these modes is potentially of some importance for both internal and extralimital dispersal, although their relative importance is undoubtedly unequal. Ambulation is evidently the predominant locomotory mode for all Nebria; and it seems reasonable to suggest that it is also the most important active means of dispersal. Data presented above indicate that individuals are capable of traveling distances of several hundred meters per day in suitable habitat. Projected over the 'lifetimes' of individuals and of populations, the potential for dispersal through ambulation is tremendous, limited only, it would appear, by the availability and continuity of suitable habitats. Both internal and extralimital dispersal may, therefore, be mainly dependent on ambulation.

Natation itself may, at times, function as a means of dispersal, but only for taxa in which members are (at least in part) riparian. Data available at present indicate that these beetles are able to survive in and navigate on water, traits which are perhaps more important for passive (see below) than active dispersal. Active locomotion in streams is probably limited to efforts toward a return to shore after accidental or intended (see Kavanaugh and Martinko, 1972, and above) stream entry; and its importance is probably confined to internal dispersal (i.e. relocation along streambanks, within the range of a population).

So few details are known about flight among Nebria that its importance is not yet understood; and, consequently, its role in

dispersal cannot yet be estimated directly. However, some pertinent indirect evidence may be cited here. The difference in mean maximum linear extent of range (see Table 6) between taxa with fully-winged members (2150 km) and those with only short-winged members (362 km) is highly significant ($P \geq 0.99$). This suggests that taxa with fully-winged individuals can both attain and successfully occupy greater ranges than taxa with only short-winged members; and differences in both internal and extralimital dispersal capabilities are at least implicated. Of the 22 Nearctic *Nebria* taxa whose ranges overlap areas which were completely covered by Wisconsinan ice sheets, 20 are represented in these areas by populations with only fully-winged members. The two exceptional taxa are *N. diversa* and *N. kincaidi kincaidi*, both of which may have survived the Wisconsinan in coastal refugia (at least in part) very close to their present ranges (see below, section 4.2). Therefore, post-Glacial reinvasion of (i.e. extralimital dispersal to) large, glaciated areas has been achieved almost exclusively by taxa with fully-winged members. A first and most probable conclusion is, therefore, that flight is important for dispersal; and this may well be true. However, there is yet no 'proof' that flight has a role in dispersal. As suggested by B. B. Chiolino (personal communication), fully-winged individuals may simply have a greater intrinsic (behavioral) tendency to disperse than short-winged individuals; and it is still possible that, in fact, they walk rather than fly.

Passive dispersal.--Several classes of carriers may be involved in passive dispersal. Of those discussed by Udvardy (1969), the following may contribute to the dispersal of *Nebria*: anemochore dispersal (i.e.

dispersal by wind or air currents); anthropochore dispersal (i.e. dispersal by or with man); and hydrochore dispersal (i.e. by moving water). I exclude biochore dispersal (i.e. dispersal by other organisms) because the kinds of interactions with other organisms normally considered prerequisite for this mode of dispersal are unknown among Nebria.

It is doubtful that any foreseeable circumstances would permit Nebria individuals to be picked up off the ground by air currents or wind in the microhabitats they occupy. However, because at least some Nebria adults fly, anemochore dispersal is possible. Nothing is known about flight characteristics of these beetles, however, so that a reasonable estimate of the likelihood of passive aerial dispersal is yet impossible. I find no distributional anomalies among Nearctic Nebria the explanation of which require hypotheses of anemochore dispersal (see section 4.2 below).

Anthropochore dispersal has played no apparent role in the dispersal of Nearctic Nebria. This is not surprising, because members of these species occupy microhabitats not yet extensively exploited by man or containing materials or plants routinely transported by him. [Lindroth (1957 and 1963a) reviewed the characteristics of habitats occupied by carabid beetles frequently transported by man]. It is possible that riparian beetles could be transported (as adults, larvae or eggs) in sands and gravels mined from active stream beds. However, most (and all large-scale) sand/gravel mining operations in North America have worked from quarries (i.e. 'fossil' stream beds) rather than live streams (Kaiser Sand and Gravel representatives, San Francisco; personal communication). Furthermore, successful dispersal

of these riparian beetles would require that materials taken from one stream be deposited in proximity of another. As demonstrated by Lindroth (1957), introductions of riparian carabids are improbable events.

The two N. brevicollis records for North America (see Appendix B and species description) no doubt represent independent accidental ("adventive") introductions by man. N. brevicollis members are highly synanthropic in Europe. Individuals are common in gardens and parks and are totally independent of streams or other water bodies. Transport of adults, larvae or eggs in potted plants or soil, for example, would seem quite possible.

One last, and potentially most important, role for man in aiding and/or directing the dispersal of Nebria may be through his alterations of drainage systems--by diverting streams themselves to new channels, redirecting water flow through aqueducts or canals (thereby possibly linking previously discrete drainage systems) or by constructing bridges (see discussions of trollism above, section 3.2311, and below). These activities may facilitate dispersal, but only indirectly, in concert with ongoing passive dispersal in water.

Because a majority of Nebria taxa have members associated with water systems, including rivers and the creeks, rivulets, springs, snowfields and glaciers which feed them, hydrochore dispersal undoubtedly is and has been an important mode for present and past dispersal in this group. Downstream drift of riparian and, perhaps, perinival beetles is probably (see below for evidence of extralimital dispersal along streams) very common. Profound changes in distribution are possible when passive dispersal in streams is coupled with geologic

and hydrographic events (including those affected by man) which alter the location or direction and volume of stream flow. Classes of natural events of probable present or past importance for Nebria dispersal include orogeny, regional uplift and tilt, embayment (damming) of rivers by lava flows, glaciers or ice sheets (followed by rechannelization) and stream capture (see section 4.2 for discussion of Nebria distributions in relation to these events).

Some of the more classic examples of hydrochore dispersal involve crossings of more extensive water gaps (e.g. stretches of ocean or lake between mainland and islands) and employ various forms of rafting (e.g. ice rafting, rafting on or in logs or other floating debris). Few Nearctic Nebria members are likely to be involved in such dispersals because their habitat preferences provide few or no such opportunities. Members of few taxa (e.g. N. lacustris lacustris) are associated with the shores of large lakes. Only N. diversa and N. gregaria members are common seashore inhabitants and, therefore, likely to participate in and survive extralimital dispersal in or on the surface of seawater. Most Nebria, and all those associated with riparian or sea strand habitats prefer areas free of vegetation and are therefore unlikely to be transported by rafts originating in their areas. The only Nearctic Nebria distribution for which an explanation appears to require oversea dispersal on water is that of N. gregaria (see section 4.2). All members of this species are short-winged; and their presence on various of the Aleutian Islands can be most reasonably explained by this passive means, unless present estimates of sea level changes in Pleistocene time are grossly in error (Lindroth, 1963b). A possible role for ice rafting in Nebria dispersal can be neither excluded nor

supported at present. It is, however, unlikely that individuals could survive on such rafts unless soil and rock were present on top of at least part of the raft.

Short-range passive dispersal on or in water or on ice appears to pose no severe behavioral, metabolic or physiological problem for members of many Nebria taxa. As noted above, riparian beetles are competent surface swimmers, and some readily enter water at temperatures near freezing. Perinival beetles can tolerate near-freezing temperatures nightly. Low water temperatures, known to immobilize and/or kill some carabids (e.g. Scaphinotus (Brennus) spp. members, personal observations), may have no negative effect on Nebria members. Many Nebria, therefore, appear to be quite well-adapted for hydrochore dispersal in cool or cold streams.

My own field observations on adults of several Nebria species suggest an additional behavioral characteristic of special advantage for hydrochore dispersal. When suddenly thrown into streams, adults will often float to the surface and assume a compact floating posture (Fig. 364), with all appendages tucked close to the body. They remain motionless (even if floating upside down) until the current propels them against the shore or some emergent stone. The swifter the current, the more likely the beetles are to remain inactive. Some begin swimming actively in calmer water before they reach stones or shore. Such behavior may conserve much energy, thereby permitting longer dispersal and greater chance of survival.

Internal dispersal

Movements of individuals within the distributional limits of their

respective populations or taxa have not yet been studied for any Nearctic Nebria. Greenslade (1964a) used pitfall traps and mark-release-recapture techniques to study movements of N. brevicollis adults within and between each of two beech litter plots at Silwood Park (England). Areas of the two plots were, respectively, 1700 m^2 and 85 m^2; and distance between them was 45 m. He found that, during the seasonal periods of locomotory activity for members of this species, movement within the larger plot was "constant," even for undisturbed (see above) adults, but that exchange of adults between plots was very low (only one percent of undisturbed adults moved from the larger to the smaller plot). This suggests that, where preferred microhabitat areas are discontinuous, although separated by relatively small gaps, movement of individuals may be greatly restricted and confined to small areas. I am at present unable to accurately assess the role of various active and passive dispersal means in internal dispersal, but suggest that ambulation is of primary importance.

Migration is a special kind of internal dispersal. As noted above (section 3.231), migrations presently known among Nearctic Nebria are limited to short-range seasonal movements associated with melting snowfield margins and rising and falling stream levels. I have no data which suggest that Nebria individuals have a "home range" or routinely return to a particular spot after a period of locomotory activity. Movements associated with the above migrations appear to be only ambulatory.

Extralimital dispersal

Carabid beetles which readily fly are frequently found in areas

outside the normal ranges of their populations or even their taxa. Darlington (1943) noted that fully-winged members of several lowland carabid species are sometimes collected at the crest of the Presidential Range (New Hampshire). No such records can yet be cited for Nearctic Nebria members.

Examples of extralimital dispersal among Nebria (except for the apparent anthropochore dispersal of N. brevicollis members to North America from Europe; see above) are more subtle and restricted to downstream drift events (hydrochore dispersal). Spence (1974) occasionally found both adults and larvae of N. pallipes and N. lacustris lacustris along streams at elevations below those normally occupied by members of these species, especially after rains. As noted above (section 3.2311), I have frequently found adults of different Nebria taxa under bridges at elevations well below the altitudinal ranges of their respective taxa. Bridges provide suitably cool, shaded areas in which the beetles can survive after displacement from their normal ranges; and they therefore serve to preserve records of passive extralimital dispersal. As suggested by the surprising frequency of this trollism and the likelihood that only a small percentage of displaced individuals reach these safe shelters, the number of individuals dispersing passively downstream must be very large.

It is interesting to speculate on the potential role of bridges and, therefore, trollism in successful extralimital dispersal of riparian Nebria. On a geologic timescale, bridges are certainly new features of the environment; and no role in past dispersals can reasonably be assigned to them. However, 'natural' equivalents of bridges along streams are few and most are quite small. The closest

equivalent might be an undercut stream bank; but this would be spatially and temporally quite limited and a very dangerous place to be during even minor flooding. As more and larger bridges are built, their cumulative effect on present and future Nebria dispersal may be important. The streambank areas shaded by some existing bridges (especially the new bridges of the interstate highway system which carry six traffic lanes or more) are very large. Some of the areas I have examined under bridges, for example, are more than 3000 m^2. Given even a moderate immigration rate through hydrochore dispersal from areas upstream, large, permanent populations could become established in these areas and, in turn, serve as a source for new colonization under bridges further downstream.

One particular area in North America worth watching in the future for possible effects of trollism is that portion of the Columbia River system which includes the lower Columbia River and the Snake River. From the source of the Snake River in Yellowstone National Park (Wyoming) to the mouth of the Columbia River at the Pacific Ocean, this watercourse passes through and receives drainage from three distinct Nebria faunal regions. Each region is separated from the others by low, arid areas which have evidently served as barriers to dispersal in post-Glacial time (see section 4.2). A recent westward dispersal of eastern elements along this watercourse is not yet strongly indicated in the Nebria fauna; but as more large bridges continue to dot the intervening lowlands, some net westward shift of eastern elements might be expected.

I have not yet observed any special behavior patterns in any Nebria members (except, perhaps, in members of N. ingens; see above,

section 3.2341) which would tend to reverse downstream displacement. One such pattern would be a tendency to walk or fly upstream. If some such mechanism evolves (or, in fact, already exists) among *Nebria*, then beetles displaced down one stream might reverse direction and actively disperse up a different stream. Aided by downstream drift and suitably positioned microhabitat islands (under bridges), beetles could then disperse across lowland barriers and invade new tributaries and mountain ranges, which in the area discussed above, could lead to extensive faunal mixing.

3.24 Paleontology

The study of fossil specimens and their temporal and spatial distribution may provide valuable data on the evolutionary histories of taxa and biota and on past climate and geography. Hennig (1966) noted that evidence on "phylogeny" of characters (i.e. polarity of character transformations) can, at times, be obtained from stratigraphic sequences (his "paleontological method") (see Matthews, 1970 and 1976 for superb examples). Recently, several proponents of cladistic systematics (e.g. Schaeffer _et al._, 1972; and Cracraft, 1974) have questioned various traditional uses of paleontological data, especially (1) in the search for actual "ancestors" of extant taxa and (2) in the use of stratigraphic sequence data to determine, _a priori_, character transformation polarity. There seems to be no doubt, however, that structural, temporal and distributional data from fossils can be extremely important in the testing and reformulation of hypotheses about relationships, character transformations and distributional histories of taxa, if evolutionary theory and knowledge of the inherent limitations (and bias) of these data serve as constraints on interpretation of their significance.

Fossil specimens of any age can be useful in systematics; but those representing extant taxa have added importance. By applying the principle of 'uniformitarianism' and knowledge of the present environmental relations and requirements of members of these taxa to study of these fossils, the latter can be used in reconstructions of past environments. More importantly for the present study, however, such specimens record the location and, perhaps, some structural

characteristics of members of an extant taxon at some point in past geologic time (assuming that we can, in fact, assign the specimens to some extant taxon). These data may bear directly on interpretation of past distribution and minimum age of a taxon.

Review of Nebria fossils

The fossil record for Nebria to date is very poor--limited in diversity, distributional representation and geologic time span covered. The oldest fossil clearly representative of some Nebria taxon is of Pliocene age, far too recent to be of any significance in elucidating the early history of the genus. Because specimens were too fragmentary and/or because they could not be distinguished from equivalent specimens representing extant taxa, I obtained no data pertinent to analyses of character transformations or relationships among past or present Nebria faunas. Data pertinent to considerations of the minimum ages and past distributions of extant taxa are discussed with respective species descriptions (section 3.43) and in section 4.23 on historical zoogeography.

Tertiary fossils.--S. H. Scudder described two Nebria species from Tertiary deposits. Nebria paleomelas Scudder (1879:173B; see also 1890:532, 1895a:54 and 1900:17) was described from "Tertiary" beds ("below main coal seam") at Nicola River, British Columbia. Nebria occlusa Scudder (1900:17) is from the Florissant Beds (Florissant, Colorado) of Miocene age. I have not yet studied either of these specimens. However, Scudder's descriptions match details of his drawings for both the N. paleomelas (Scudder, 1890:Pl. 2, Fig. 20) and the N. occlusa (Scudder, 1900:Pl. 1, Fig. 3) specimens. Based on

characters of the elytral striae (including length and position of the scutellar striole and the relationship between the bases of striae 1. and 2.) (see section 3.21 above on comparative morphology for details), I conclude that the specimens described and illustrated do not represent Nebria species. [Both probably represent Amara species.]

The only North American Tertiary fossil presently referable to genus Nebria is that collected by J. V. Matthews, Jr. (see Hopkins et al., 1971; and Matthews, 1977)from the Lava Camp mine (Inmachuk River valley, Seward Peninsula, Alaska). The specimen (Fig. 91) is of Pliocene age (ca. 5.7 million years B. P.), consists of an almost complete left half of a pronotum, and is structurally indistinguishable from the pronotum of a living N. nivalis nivalis adult. Members of N. nivalis (Holarctic distribution) and all other species (all are restricted to the Palaearctic Region) of the nivalis species subgroup (see below, section 3.32) are uniquely characterized by the presence of a small, longitudinal tubercle on the lateral pronotal explanation medial to the midlateral seta. The identity of this specimen, however, as representing N. nivalis nivalis, or some extinct member of the nivalis species subgroup or, more specifically, the stem species of the nivalis species subgroup or any part thereof cannot possibly be established.

Quaternary fossils.--Fortunately, Nebria fossils of Pleistone and post-Glacial age are relatively abundant, from both Eurasia and North America; and the use of modern techniques for recovery of specimens and the expertise and enthusiasm of present investigators (cited below) should help to provide much more material in the future.

Fossil specimens of N. brevicollis are known from various deposits in the British Isles, including some of "Older Dryas" age (ca. 12,500 years B. P.) from North Wales (Coope and Brophy, 1972) and post-Glacial (?) age (ca. 10,000 years B. P.) from England (Ashworth, 1973). Nebria livida (Linnaeus) specimens have been found in Weichselian ("middle Devensian", ca. 38,500 years B. P.) deposits at Four Acres, England (Morgan, 1973). Nebria gyllenhali fossils are known from England (late Weichselian, ca. 10,670 years B. P. or less; Ashworth, 1973) and Scotland (late Allerød interstadial, ca. 11,200 to 10,900 years B. P.; Coope, 1968). Nebria nivalis nivalis specimens have been found in "Younger Dryas" (late Weichselian) deposits in England (Coope, 1970b).

North American Quaternary deposits from which Nebria specimens have been recovered to date are confined to the Toronto (Ontario) area and include the Scarborough Formation ("Scarborough Bluffs"; early Wisconsinan, ca. 70,000 years B. P. (Morgan, 1972)) and the Don Formation ("Don Valley Brickpit"; Sangamon interglacial, ca. 100,000 years B. P. (A. Morgan, personal communication)).

Scudder (1895b:70) based his Nebria abstracta on a single elytron from Scarborough. Although I have seen only the description and illustration (Scudder, 1895b:Pl. 6, Fig. 2) of this specimen, and again based on the pattern of elytral striae (specifically the separate origins of striae 1. and 2. at the basal margin), I conclude that the specimen is non-nebriine (and probably represents an Agonum species).

Scarborough material (received for study from Anne Morgan) included elytral fragments which I have tentatively identified as representing N. suturalis (Figs. 178a,178b) and N. nivalis nivalis (Figs.180a,180b)

adults. The presumptive N. suturalis elytral specimens are similar (in microsculpture, depth and punctation of striae and shape of the elytral base) to elytra of living members of that species. The combination of character states--size medium; foveate punctures on elytral interval 5. (and, in some members, 7.) present; metallic reflection of elytra absent--is diagnostic for adults of N. nivalis nivalis (Figs. 178a and 178b).

Five elytral fragments (Figs. 179a,179b) (also received from Alan and Anne Morgan) from the Don Valley Brickpit appear to represent members of either N. lacustris lacustris or N. pallipes. Members of these two taxa, and also the fossil specimens, are similar in elytral microsculpture (meshes strongly transverse) and depth of impression of the striae. Because these taxa are broadly sympatric and their members are commonly found together at present, both may be represented among the fossil specimens. Unfortunately, all fragments lack the elytral apical area, to which the only differentiating elytral characters apply.

3.3 Classification

In this section, I discuss classification, especially in relation to evolutionary history, review the history of classification of Nearctic Nebria, and provide a reclassification of the Nearctic taxa.

3.31 Classification: a perspective

Much has been written in the last 20 years on the purposes, principles, and methods of classification. Several contemporary and competing philosophical approaches to classification can be recognized; and these have been called the "pure phenetic", "omnispective", "cladistics", and "evolutionary" approaches, respectively. A superficial review of the literature suggests that great, irreconcilable differences between them must exist. In fact, the approaches have much in common and can be properly distinguished only on more subtle points than are first apparent. All basically agree with Simpson (1961) that classification is "the ordering of [organisms] into groups on the basis of their relationships, that is, of associations by continuity, similarity or both"; and all view classifications as devices for storage and retrieval of information about organic diversity. Differences involve the kinds of relationships that are used or emphasized in formulation of the classifications.

The critical area in which these respective approaches differ is in the relationship advocates of each perceive between classification and evolutionary history. Advocates of the "pure phenetic" (e.g. Sokal and Sneath, 1963) and "omnispective" (see Blackwelder, 1967) approaches

work from the premise that evolutionary history (phylogeny in particular) is unknowable and, therefore, cannot be used as a basis for classification. Advocates of the "cladistic" (i.e. "phylogenetic" of Hennig, 1966) and "evolutionary" (e.g. Mayr, 1969; and Simpson, 1961) approaches contend that testable hypotheses on evolutionary history can be generated through appropriate handling of data on living organisms (and/or fossils); and they agree that hypotheses on evolutionary relationship should serve as the basis for classification.

Because evolutionary theory provides the unifying concept for all biology through a causal explanation of observed diversity, classifications, which are themselves intended as devices for unification and orderly arrangement and storage of information on this diversity, should, if possible, reflect evolutionary relationships. I concur with Whitehead (1972) that classifications must also have predictive value--that is, suggest relationships among members classified in characteristics not yet studied. Such predictions can often be tested directly and therefore serve, themselves, as tests of the classification. Only classifications based on evolutionary relationships can be expected to have this predictive power.

The fundamental rift between cladistic and evolutionary approaches to classification involves a difference in ranking criteria (i.e. the "absolute ranking" of Hennig, 1966) rather than grouping procedures. Griffiths (1974) has provided a conceptual framework in which this distinction is clear (see also Kavanaugh, in press C). He distinguishes between <u>classification</u> (defined above) and <u>systematization</u>, which he defines as "the ordering of organisms according to relations within a

system". He views organic diversity as a hierarchy of element/system relations--an extension of the "levels or organization" concept--and not hierarchy of classes. Systems are unique, individual wholes; and just as single cells are elements of tissues, and tissues elements of organs, populations are elements of species and species elements of a system at the next higher level of organization (e.g. genus). Species are, therefore, elements of a system which exists as an historical reality, independent of our perception of it, generated through the speciational processes of evolution. The important consequences of adopting this perspective are as follows: (1) relationships among the elements (taxa) in this system are historically determined by the branching pattern of phylogeny and are therefore independent of any criterion of similarity; and (2) because systems are themselves wholes, elements are automatically and necessarily parts of them, again without reference to any other criteria. Attempts to discover relationships within the system and to order taxa accordingly can be called "systematization". Classes, on the other hand, are abstractions, and class-membership is dependent on possession of certain essential or contingent attributes. Classification is, therefore, distinct from systematization; but to the extent that a classification mirrors the natural hierarchic system, it can reflect the same objective reality.

In terms of the above concepts, strictly cladistic classifications attempt to mirror exactly the element/system relationships perceived through systematization procedures (see section 4.1 on phylogeny for discussion and details). The formal rank of a taxon in such a classification is determined by its position in the hierarchy (e.g.

"sister" taxa [see section 4.1] are accorded equal rank) and by its geologic age (Hennig, 1966). Degree of phenetic distinctiveness is not used as a criterion for ranking, because its use would necessarily distort element/system relationships. In contrast, this criterion is used extensively in evolutionary classifications. Advocates of this approach consider divergence and novelty as important components of evolutionary history and seek to incorporate these factors in their classifications. Divergence therefore influences formal ranking. Again, as suggested by cladistics, some distortion of element/system relationships normally results from this procedure. Ashlock (1974) acknowledged this in noting the need to consider only "holophyletic" (i.e. "monophyletic", sensu Hennig, 1966) groups in zoogeographic studies.

I concur with Brundin (1966 and 1972), Griffiths (1972, 1974a, and 1974b), and Hennig (1966) that cladistic classifications are to be preferred as general reference classifications. There are, however, practical problems with such classifications. As noted by Crowson (1970) and Mayr (1969) among others, they tend to require larger numbers of categories than more traditional classifications, due to the dichotomous branching format followed in representing hypothetical ancestral relationships. For groups such as Nebria (see cladogram, Fig. 373) which demonstrate markedly unequal diversity in different lines, the resulting cladistic classification is highly asymmetrical and unbalanced with respect to the distribution of taxa in various categories. In such instances, awkwardness of the classification may offset its inherent usefulness.

Nelson (1974) discussed classification as an expression of phylogenetic relationship and presented a convention, called "sequencing", which permits a more manageable arrangement of taxa and judicious use of categories while preserving all the phylogenetic information of a strictly cladistic classification. The convention is as follows: "descendant units may be sequenced [listed] according to the order of branching of their presumed ancestry". The sequence (order) of taxa so listed is critical. A taxon listed under this convention is taken to be the sister group of that group including all the following taxa ranked at the same or lower rank. For example, if three taxa are listed in the order A, B, and C, and each is assigned genus rank, the sequence implies that A is the sister group of B and C together, and that B is the sister group of C. With knowledge of the convention, the reader can reconstruct directly the cladogram on which the classification is based. I have followed this convention in the classification presented below, thereby reducing the number of categories required to express relationship from 10 to 5, with no loss of information on presumed cladistic relationship.

3.32 History of Nearctic *Nebria* classification

LeConte (1878) was first to attempt a classification of Nearctic *Nebria* taxa. He arranged 22 species (19 [86%] of which I recognize as distinct species) in six species groups, based on the following characters: (1) number of pairs of posterior paramedial setae on third through fifth visible sterna; (2) elytral shape; (3) hindwing length; (4) length of the metepisternum; (5) pronotal shape; and (6) degree of

margination of the prosternal intercoxal process.

Casey (1913, 1920, and 1924) described numerous new species, recognized a total of 44 species (22 [49%] of which I recognize as distinct species), and rearranged LeConte's classification to accomodate these new taxa and his divergent views on relationship. He proposed seven species groups (Casey, 1913), only two of which were identical in name and composition with LeConte's (Fig. 365). The other groups differed with LeConte's in either the inclusion of new taxa or the transfer of one or more taxa from one group to another. Characters used by Casey for grouping taxa were less dependable than those used by LeConte and included: (1) elytral shape; (2) elytral convexity; (3) pronotal shape; and (4) "habitus". Casey's classification therefore represents no advance in an understanding of the relationships of Nearctic taxa.

E. C. Van Dyke was keenly interested in relationships among Nebria species and used distribution (especially vicariance) patterns among Nebria species he considered related to illustrate certain of his ideas on the origins and distributions of Nearctic insects (see Van Dyke, 1919, 1926, and 1940). Unfortunately, he did not publish his views on relationship in any manner approaching a classification; and what remains of his perspective can be seen only in scattered narrative passages (unsupported by data or analyses) (e.g. Van Dyke, 1919:8).

Following LeConte and Casey, the next classification to include Nearctic taxa was that of Bänninger (1925), who reviewed the world-wide Nebria fauna, but treated Nearctic taxa only superficially. He considered Nebria ovipennis, N. kincaidi, and N. paradisi ("N.

columbiana Casey") as members of subgenus *Nebriola* Daniel (1903) and arranged the other Nearctic species among five species groups as members of subgenus *Nebria* (= *Paranebria* Jeannel, 1937, not *Nebria* latreille, 1802). He also dealt briefly with relationships among Nearctic taxa in later papers (Bänninger, 1931, 1933, and 1949). In reworking Bänninger's classification, Jeannel (1937) removed all Nearctic taxa from subgenera *Paranebria* and *Nebriola* and reassigned them, with several Palaearctic taxa, to his new subgenus *Boreonebria*.

The most comprehensive classification of Nearctic *Nebria* to date has been that of Lindroth (1961a). He classified 40 species (36 [90%] of which I recognize as distinct species) into 12 species groups based on a diversity of characters which included: (1) presence or absence of the mid-lateral pronotal seta; (2) pronotal shape; (3) width of the lateral pronotal explanation; (4) number of setae at the base of the hind coxa; (5) presence or absence of setae on second visible abdominal sternum; (6) presence or absence of anterior paralateral setae on third through fifth visible abdominal sterna; (7) elytral shape; (8) continuity of elytral intervals; and (10) structure of the genitalia of males. Lindroth's work represents the major advance in knowledge of relationships within and composition of the Nearctic fauna; and it forms the foundation for my study presented here. It is informative to use Lindroth's classification as a standard with which to compare earlier as well as subsequent classifications. Figs. 365 and 366 graphically illustrate differences in composition of the groups proposed by LeConte and Casey, by later workers noted below, and by me in the classification proposed below, in comparison with Lindroth's

groups. Both great departure from earlier classifications and close approximation to subsequent classifications are evident for Lindroth's classification from this comparison.

Erwin and Ball (1972) revised the _trifaria_ and _ovipennis_ species groups of _Nebria_ and were first to employ cladistic and zoogeographical analyses in the study of relationships among members of the genus. They were also first to use characters of the digestive system and female reproductive system (e.g. bursa copulatrix and associated structures) in a comparative study of _Nebria_ taxa.

The most recent work on _Nebria_ classification is that of Shilenkov (1975a), who revised the genus for Siberia and far-eastern Asia. He proposed several new subgenera, two of which include a majority of the Nearctic taxa. The relationships between his classification (as it applies to Nearctic taxa) and Lindroth's and my own are represented in Fig. 366 . In general, my findings support those of Shilenkov quite closely.

3.33 A reclassification of Nearctic _Nebria_

I present here a reclassification of the Nearctic _Nebria_ taxa, based on detailed phylogenetic (cladistic) and zoogeographic analyses which are presented in sections 4.1 and 4.2, respectively, below. Every effort was made to maintain independence of these two analyses, so that, in the end, hypotheses generated from zoogeographic analysis could be used in objective tests of hypotheses on relationship generated from cladistic analysis. The resultant compatibility of cladistic and historical zoogeographic reconstructions is discussed in

section 4.3 below.

The cladogram on which the classification is based is presented in Fig. 373 . As noted above, the branching pattern of the cladogram is highly asymmetrical--a bonsai among "family trees". I therefore applied the sequencing convention discussed above to obtain a more balanced distribution of taxa over the categories used, with no loss of cladistic information.

I have refrained from naming or recognizing subgenera at this time, and prefer to wait until a reclassification of the world fauna is possible before doing so. All supraspecific relationships within *Nebria* are not yet apparent; and there is no need to add to the long list of formal names already proposed for major subdivisions of *Nebria*. These names are simply listed as synonyms of *Nebria* Latreille (see section 3.41) and are not discussed further.

I use the informal rank of "lineage" as the most inclusive category within genus *Nebria*. For reference purposes only, I note that lineages recognized here will probably be ranked either as subgenera or genera when the classification is eventually upgraded to include the world-wide fauna. In fact, Shilenkov (1975a) has already proposed subgenera which correspond almost exactly to the *gyllenhali*, *gregaria*, and *metallica* lineages I recognize; and Habu (1958) has ranked the group comprising the Palaearctic members of the *virescens* lineage as a distinct genus, *Nippononebria* Ueno.

Because the criterion of strict monophyly of groups (Hennig, 1966) requires inclusion of *all* descendants of a common ancestor as well as only them (see below, section 4.1), I examined all

available Palaearctic material in a search for representatives of taxa possibly related to Nearctic forms. A total of 20 such taxa were found represented (and three more taxa, members of which I have not yet examined, may be related to Nearctic taxa). These representatives were included in the cladistic and zoogeographic analyses and appear in the cladogram (Fig. 373). In fact, seven of the 10 species groups recognized have Palaearctic representatives. However, I have omitted the Palaearctic taxa from the classification as outside its scope.

A CLASSIFICATION OF NEARCTIC *NEBRIA* SPECIES

A. The *virescens* lineage

   I. The *virescens* group

      1. *N. virescens* Horn

B. The *gyllenhali* lineage

   I. The *paradisi* group

      1. *N. paradisi* Darlington

   II. The *hudsonica* group

      1. *N. gouleti* Kavanaugh, new species

      2. *N. hudsonica* LeConte

      3. *N. lacustris* Casey

         a. *N. lacustris lacustris* Casey

         b. *N. lacustris bellorum* Kavanaugh, new subspecies

   III. The *gyllenhali* group

      A. The *nivalis* subgroup

         1. *N. nivalis* (Paykull)

            a. *N. nivalis nivalis* (Paykull)

            b. *N. nivalis gaspesiana* Kavanaugh, new subspecies

      B. The *gyllenhali* subgroup

         1. *N. crassicornis* Van Dyke

            a. *N. crassicornis crassicornis* Van Dyke

            b. *N. crassicornis intermedia* Van Dyke

         2. *N. gyllenhali* (Schönherr)

a. *N. gyllenhali castanipes* (Kirby)

b. *N. gyllenhali lassenensis* Kavanaugh, new subspecies

c. *N. gyllenhali lindrothi* Kavanaugh, new subspecies

3. *N. frigida* Sahlberg

C. The *gregaria* lineage

I. The *gregaria* group

A. The *lyelli* subgroup

1. *N. lyelli* Van Dyke

2. *N. acuta* Lindroth

a. *N. acuta acuta* Lindroth

b. *N. acuta quileute* Kavanaugh new subspecies

B. The *sahlbergii* subgroup

1. *N. sahlbergii* Fischer von Waldheim

a. *N. sahlbergii sahlbergii* Fischer von Waldheim

b. *N. sahlbergii modoc* Kavanaugh, new subspecies

c. *N. sahlbergii triad* Kavanaugh, new subspecies

C. The *gregaria* subgroup

1. *N. gregaria* Fischer von Waldheim

2. *N. charlottae* Lindroth

D. The *arkansana* subgroup

1. *N. arkansana* Casey

a. *N. arkansana arkansana* Casey

b. *N. arkansana edwardsi* Kavanaugh, new subspecies

c. *N. arkansana oowah* Kavanaugh, new subspecies

d. *N. arkansana uinta* Kavanaugh, new subspecies

2. *N. fragilis* Casey

a. *N. fragilis fragilis* Casey

b. N. *fragilis teewinot* Kavanaugh, new subspecies

3. *N. zioni* Van Dyke

a. *N. zioni zioni* Van Dyke

b. *N. zioni oasis* Kavanaugh, new subspecies

II. The *obliqua* group

A. The *obliqua* subgroup

i. The *obliqua* infragroup

1. *N. suturalis* LeConte

2. *N. obliqua* LeConte

ii. The *pallipes* infragroup

1. *N. appalachia* Darlington

2. *N. pallipes* Say

III. The *mannerheimii* group

A. The *mannerheimii* subgroup

1. *N. darlingtoni* Kavanaugh, new species

2. *N. mannerheimii* Fischer von Waldheim

B. The *eschscholtzii* subgroup

i. The *desolata* infragroup

1. *N. desolata* Kavanaugh

2. *N. navajo* Kavanaugh, new species

ii. The *eschscholtzii* infragroup

1. *N. eschscholtzii* Menetries

2. *N. diversa* LeConte

D. The *metallica* lineage

I. The *ovipennis* group

A. The *gebleri* subgroup

1. *N. gebleri* Dejean

a. *N. gebleri gebleri* Dejean

b. *N. gebleri cascadensis* Kavanaugh, new subspecies

c. *N. gebleri rathvoni* LeConte

d. *N. gebleri siskiyouensis* Kavanaugh, new subspecies

e. *N. gebleri strawberriensis* Kavanaugh, new subspecies

B. The *ovipennis* subgroup

i. The *kincaidi* infragroup

1. *N. carri* Kavanaugh, new species

2. *N. kincaidi* Schwarz

a. *N. kincaidi kincaidi* Schwarz

b. *N. kincaidi balli* Kavanaugh, new subspecies

ii. The *ovipennis* infragroup

1. *N. spatulata* Van Dyke

a. *N. spatulata spatulata* Van Dyke

b. *N. spatulata sierrae* Kavanaugh, new subspecies

2. *N. ovipennis* LeConte

II. The *metallica* group

A. The *meanyi* subgroup

1. *N. meanyi* Van Dyke

a. *N. meanyi meanyi* Van Dyke

b. *N. meanyi lamarckensis* Kavanaugh, new subspecies

c. *N. meanyi sylvatica* Kavanaugh, new subspecies

B. The *metallica* subgroup

i. The *metallica* infragroup

1. *N. metallica* Fischer von Waldheim

III. The *trifaria* group

A. The *ingens* subgroup

1. *N. ingens* Horn

a. *N. ingens ingens* Horn

b. *N. ingens riversi* Van Dyke

2. *N. vandykei* Bänninger

a. *N. vandykei vandykei* Bänninger

b. *N. vandykei wyeast* Kavanaugh, new subspecies

B. The *schwarzi* subgroup

1. *N. piperi* Van Dyke

2. *N. schwarzi* Van Dyke

   a. *N. schwarzi schwarzi* Van Dyke

   b. *N. schwarzi beverlianna* Kavanaugh, new subspecies

C. The *trifaria* subgroup

i. The *purpurata* infragroup

1. *N. purpurata* LeConte

ii. The *trifaria* infragroup

1. *N. trifaria* LeConte

   a. *N. trifaria trifaria* LeConte

   b. *N. trifaria catenata* Casey

   c. *N. trifaria utahensis* Kavanaugh, new subspecies

2. *N. coloradensis* Van Dyke

3. *N. piute* Erwin and Ball

3.4 Nomenclature, Description and Identification

3.41 Genus *Nebria* Latreille

Nebria Latreille, 1802:89. *Type species*.--*Carabus brevicollis* Fabricius, 1792:150 (by subsequent designation; Latreille, 1810: 68).

Alpaeus Bonelli, 1810:68. *Type species*.--*Carabus hellwigi* Panzer, 1797: 107 (by original designation).

Helobia Curtis, 1826, pl. 103. *Type species*.--*Carabus brevicollis* Fabricius, 1792:150 (by original designation).

Eurynebria Ganglbauer, 1891:134. *Type species*.--*Carabus complanatus* Linnaeus, 1767:671 (by original designation).

Oreonebria K. Daniel, 1903:159 (as a subgenus of *Nebria*). *Type species*. *Alpaeus castanea* Bonelli, 1810:75 (by subsequent designation; Jeannel, 1937:2).

Nebriola K. Daniel, 1903:164 (as a subgenus of *Nebria*). *Type species*.-- *Nebria laticollis* Dejean, 1826:244 (by subsequent designation; Jeannel, 1937:3).

Epinebriola K. Daniel and J. Daniel, 1904:77 (as a subgenus of *Nebria*). *Type species*.--*Nebria oxyptera* K. Daniel and J. Daniel, 1904:75 (by monotypy).

Spelaeonebria Peyerimhoff, 1911:359 (as a subgenus of *Nebria*). *Type species*.--*Nebria nudicollis* Peyerimhoff, 1911:359 (by monotypy).

Psilonebria Andrewes, 1923a:275 (as a subgenus of *Nebria*). *Type species*.--*Nebria superna* Andrewes, 1923a:273 (by monotypy).

Patrobonebria Bänninger, 1923:131 (as a subgenus of *Nebria*). *Type*

species.--*Nebria desgodinsi* Oberthür, 1883:47 (by subsequent designation; Jeannel, 1937:2).

Eonebria Semenov-Tian-Shanskij and Znojko, 1928:213 (as a subgenus of *Nebria*). *Type species*.--*Nebria komarovi* Semenov-Tian-Shanskij and Znojko, 1928:214 (by original designation).

Eunebria Jeannel, 1937:3 (as a subgenus of *Nebria*). *Type species*.--*Carabus psammodes* Rossi, 1792:85 (by original designation).

Boreonebria Jeannel, 1937:4 (as a subgenus of *Nebria*). *Type species*.--*Carabus rufescens* Ström, 1768:331 (= *Carabus gyllenhali* Schönherr) (by original designation).

Paranebria Jeannel, 1937:4 (as a subgenus of *Nebria*). *Type species*.--*Carabus lividus* Linnaeus, 1758:414 (by original designation).

Neonebria Hatch, 1939b:84 (as a subgenus of *Nebria*). *Type species*.--*Carabus lividus* Linnaeus, 1758:414 (by original designation).

Nebriorites Jeannel, 1941:199 (as a subgenus of *Oreonebria*). *Type species*.--*Alpaeus gagates* Bonnelli, 1810:74 (by original designation).

Alpaeonebria Csiki, 1946:166 (as a subgenus of *Nebria*). *Type species*.--*Nebria fuscipes* Fuss, 1850:16 (by original designation).

Nippononebria Ueno, 1953:59 (as a subgenus of *Nebria*). *Type species*.--*Nebria pusilla* Ueno, 1953:59 (by original designation).

Orientonebria Shilenkov, 1975a:833 (as a subgenus of *Nebria*). *Type species*.--*Nebria coreica* Solsky, 1875:254 (by original designation).

Reductonebria Shilenkov, 1975a:834 (as a subgenus of *Nebria*). *Type species*.--*Nebria ochotica* R. F. Sahlberg, 1844:15 (by original

designation).

Catonebria Shilenkov, 1975a:836 (as a subgenus of Nebria). Type species.--Carabus nitidulus Fabricius, 1801:184 (by original designation).

Notes on nomenclature. In his original description of Nebria, Latreille (1802) assigned three species to the genus: Carabus brevicollis Fabricius, Carabus complanatus Linnaeus, and Carabus sabulosus Fabricius (= Carabus lividus Linnaeus). In 1810, he designated C. brevicollis as the type species of Nebria. This was an unfortunate choice, because members of this species are not typical of those of most Nebria species. Several authors (e.g. Bänninger, 1925) refused to accept C. brevicollis as the type species, and referred it instead to subgenus Helobia Stephen (1826) as the type species of that taxon. These authors considered Carabus lividus Linnaeus as the type species of subgenus Nebria. Andrewes (1935) noted this nomenclatural dilemma and suggested that Latreille's (1810) type designation be ignored and C. lividus Linnaeus accepted as type species of Nebria. Both Jeannel (1937) and Hatch (1939b) took issue with this view, each reaffirmed Latreille's type designation, and each proposed a new subgenus to accomodate C. lividus Linnaeus and its relatives [i.e. Paranebria Jeannel (1937) and Neonebria Hatch (1939b)]. Helobia Stephen is therefore an objective junior synonym of Nebria Latreille, with C. brevicollis the type species of each.

Derivation of genus name.--Greek, *nebris* = deer skin; probably in reference to the patterned tan and brown coloration of members of two originally included species (*N. complanata* (Linnaeus) and *N. livida* (Linnaeus)).

Diagnostic combination.--Head of adults with one pair of supraorbital setae; mandibular scrobe unisetose; maxillae, mentum and submentum without setiferous spiniform processes or ridges; mentum with tooth present, truncate or bifid; elytron with nine complete striae, scutellar striole short, present on basal one-third only, internal plica simple, keel-like, extended to but not across epipleuron; front coxal cavities uniperforate, separate, open posteriorly; front tibia with apex obliquely truncate, both spurs apical, antenna cleaner simple, sulcate; middle coxal cavities disjunct, confluent; basal tarsomeres of middle tarsus (both sexes) without pads of adhesive hairs ventrally; hind coxal cavities conjunct, confluent; metepimeron absent; parameres of male asetose; internal sac without spines, teeth, or plates; common oviduct without sclerites.

Description of form and structure of adults.--Size medium to medium-large, standardized body length 6.7 to 14.9 mm(in Nearctic species). Form slender, slightly convex; head and pronotum proportionally small, but varied in relative length and width; elytra proportionally large.

Color. Extremely varied; head, pronotum, elytra, and venter usually concolorous (but some individuals of some species with relatively paler elytra; some Palaearctic species with patterned elytra), pale yellow to black; antennae, mouthparts, and legs

concolorous with body or only slightly paler in most adults, but markedly contrasting (paler) in some. Head with or without pale median spot or pair of para-medial spots on frons.

Reflection. Dorsum varied, from entirely non-metallic to markedly metallic (blue, green, violet, or brassy; golden or copper in adults of a few taxa), especially on elytra, on head of members of very few species; venter of adults of most taxa and appendages of those of all taxa non-metallic.

Luster. Dorsum varied, from very dull to very shiny, faintly iridescent in adults of a few taxa.

Microsculpture. Head with isodiametric, unbroken meshes, moderately impressed to effaced, best developed on labrum of most adults; alveolae flat. Pronotum with isodiametric (slightly transverse in some adults), unbroken to slightly broken meshes, in members of some taxa arranged in rows, markedly to faintly impressed, slightly effaced in few adults; alveolae flat to slightly convex. Elytra with isodiametric to markedly transverse, unbroken to moderately broken meshes, in members of some taxa arranged in rows (reduced to dense transverse lines in few adults), markedly to slightly impressed; alveolae flat to slightly convex.

Head. Prognathous frons smooth medially (in few adults sparsely punctulate or punctate), usually faintly rugulose laterally, moderately convex to flattened medially; frontal lobes obsolete; one supraorbital seta positioned just medial to posterior margin of each eye; frontal furrows relatively short (in some adults present only as foveae), vaguely to sharply impressed (absent from a few adults). Genae not to

markedly swollen posterior to eyes. Vertex smooth, convex, with or without very faint medial fovea or more broadly transverse depression. Head not or moderately constricted posterior to eyes. Occiput not to markedly swollen (width across occiput less than to greater than width of head across eyes). Compound eyes moderately to markedly convex (flattened in adults of a few taxa), size medium to small. Antennae length moderate to very long, with basal four antennomeres without pubescence (except at apex of fourth antennomere in very few adults); scape short to long, shape varied (straight to bent, cylindrical to markedly narrowed basally and/or apically), with a single subapical seta on anterodorsal surface; pedicel with a single ventro-apical seta (with one to three additional apical setae in very few adults); second through fourth antennomeres cylindrical (laterally compressed near base in adults of few taxa); fifth through eleventh antennomeres cylindrical (in some adults slightly flattened), relatively short and broad to very elongate and slender. Clypeus with single pair of mid-lateral setae, anterior margin slightly concave (in few adults emarginate) to almost truncate; frontoclypeal suture evident, markedly impressed. Labrum with three pair of setae across apex (except in *N. complanata* (Linnaeus) adults), shape apical margin varied from slightly concave to slightly convex or bisinuate (deeply emarginate in members of very few taxa). Mandibles with well-developed, unisetose scrobes, laterally slightly to moderately explanate, medial cutting edges basally not or variously toothed (see section 3.212 above for details); apex right mandible narrow, pointed, but not hooked; apex left mandible markedly to very markedly hooked. Maxilla: stipes with all setae not

inserted on ventro-lateral spiniform processes. Labium: ligula longitudinally carinate medioventrally, with one pair of setae apicomedially, apical margin truncate to markedly toothed medially (ligula of N. complanata adults is unique in form and setal pattern); paraglossae adnate, fused to ligula (or distinct, as a very short, dentiform lobe at apicolateral corner of ligula); penultimate labial palpomere bi- or trisetose, length less than or equal to length of terminal palpomere (except in N. complanata adults). Mentum (Fig. 64) deeply emarginate anteriorly (depth of emargination varied, from one-third to one-half total length of mentum), with medioapical tooth of varied shape (bifid to broadly truncate) and length (one-third to one-sixth of depth of emargination), and with three (in few individuals two) pair of setae (one pair at base of mental tooth (M_1), one pair at basolateral angles (or absent) (M_3), and one paramedial pair at or anteriorly removed from base(M_2); each epilobe asetose apically, moderately broad, (narrowed laterally in few adults) with lateral margin smoothly rounded, and with minute to long, well-defined apical tooth. Gula T-shaped, with one to seven pairs of lateral setae not inserted in spiniform processes and zero to two pairs of medial setae not inserted in a raised, transverse medial ridge (Figs. 79 - 81).

Prothorax. Pronotum, shape slightly to very markedly cordate (in members of few taxa semiovoid, not narrowed basally); disc smooth (in few adults faintly punctulate), slightly to markedly convex; apical margin moderately convex to slightly concave medially; lateral margin slightly to markedly arcuate, with basal sinuation absent or shallow to very deep and varied in length; lateral explanation narrow to wide

throughout or anteriorly and/or posteriorly widened or narrowed; basal margin short to long, straight or variously modified; apical angles short to long and projected anteriorly, width broad to narrow, apices broadly rounded to bluntly pointed; basal angles obtuse to acute, in some adults laterally or posteriorly denticulate or projecting; apical margination markedly to faintly impressed (absent from only few adults), width moderate to narrow, present only in lateral thirds (medial one-third unmargined); lateral bead markedly to faintly impressed, wide to narrow, complete in most adults (but obliterated basally in some), widened apically or basally in many; basal margination absent; anterior transverse impression shallow to deep (absent from very few adults), broad and faintly defined to narrow and sharply defined, smooth to densely punctate; median longitudinal impression shallow to deep, smooth to moderately rugulose, varied in length but complete from apical to basal margin in very few adults; posterior transverse impression deep, narrow (broad in few adults), smooth to densely punctate, straight to anteriorly deflected at middle; basal foveae parallel to posteriorly divergent, deep (in few individuals slightly shallow), broad to narrow, smooth to moderately punctate, not or slightly extended anteriorly onto disc, lateral convexity absent to moderately carinate; a single pair of mid-lateral setae absent or present (positioned lateral to an associated small, longitudinal tubercle in members of few species); single pair of basolateral setae present (absent from adults of two species) at basal angles. Prosternum smooth to moderately punctate; intercoxal process smooth (rarely faintly punctulate or rugulose), asetose ventrally, margination complete to present basally only, shape

sublanceolate to lanceolate (rarely spatulate). Proepisternum smooth to faintly punctate. Proepimeron smooth to densely punctate. Front coxal cavities open, uniperforate, confluent.

Pterothorax. Scutellum small, visible. Elytra with silhouette varied, rectangular to almost petiolate, moderately flat to moderately convex, without pubescence; basal margination short to long, straight to markedly concave, smooth to wavy, deeply impressed and complete; humeral angles variously shaped, bluntly rectangular to markedly rounded (completely obliterated and flattened in members of very few taxa), with or without transverse humeral (epipleural) carina or tooth at the angle; subhumeral lateral sinuation absent to moderately deep; lateral explanation narrow to moderately broad, narrowed basally in most adults; subapical carina varied in length, slightly to markedly developed (absent from very few individuals); apices variously shaped, narrowly to broadly rounded or blunted, medially straight to sinuate; internal plica simple, keel-like, extended to but not across epipleuron; scutellar striole present, short, confined to basal one-third of elytron or less, not fused distally with first stria; eight complete striae, shallowly to deeply impressed (lateral striae in some adults less distinctly so than more medial striae), faintly punctulate to moderately punctate; first and second striae divergent from common stem at some distance from basal margination (in only few individuals divergent from a common point at basal margination or completely independent basally; intervals approximately equal in width, smooth (impunctate), flat to very markedly convex, continuous or faintly to markedly catenate (only third, fifth, seventh, and/or ninth in few adults) intervals interrupted

(in apical half in most instances) by shallow to deep foveae with interfoveal areas nor or moderately tuberculate); discal setiferous pores absent or indistinct to broadly (broader than width of interval) foveate; basal (scutellar) pore absent or present; third interval with one to ten setae (none in N. nudicollis Peyerimhoff adults); fifth and seventh intervals with zero to nine setae each; ninth interval with eight to 22 setae (up to 32 in N. complanata adults) (umbilicate series), not arranged into groups. Metathoracic wing size varied, large and functional with full venation pattern (Fig. 181) to reduced to small scale-like lobe with reduced venation pattern; oblongum cell present (in full to moderately short wings), shape varied (Fig. 197 - 200), broad to narrow, posterior angle slightly to markedly acute, terminated in minute to short stalk; wedge cell (Figs.201 - 205) single (absent from or double in very few individuals), triangular, truncate proximally (rectangular, open distally in few adults); marginal cell between P + Cu_2 and E_1 veins (Ward, unpublished manuscript) without sclerotized microtrichial field. Metepisternum smooth to moderately punctate. Metepimeron absent (or at least not visible externally). Middle coxal cavities disjunct, confluent. Hind coxal cavities conjunct, confluent, delimited laterally by metepisternum and first visible abdominal sternum.

Legs. Long and slender in most adults (but varied relatively among species, from long and very slender to short and robust). Front coxa globose, asetose. Middle coxa (Fig. 221) globose, with one (in few adults two) anteromedial seta and one (in few adults two) anterolateral seta subapically. Hind coxa (Figs. 223 - 229) flattened,

transverse, but not extended to lateral margin of venter; coxal ridge complete; plane of lateral wing posterior to coxal ridge 45° to almost 90° (in latter, obscured ventral aspect); one to seven basal setae and and one apical seta (with one or more extra apical setae in members of a few taxa) (Figs.226 - 227). Front and middle trochanters wedge-shaped, each with a single apico-ventral seta. Hind trochanter lobate, asetose. Front tibia with apex (Fig. 236) obliquely truncate (lateral angle displaced proximally), both spurs apical; antenna cleaner (Fig. 236) simple, symmetrical, sulcate. Middle tibia varied dorsally, flat or slightly convex to markedly concave and sulcate (especially in distal half), with slightly to moderately developed longitudinal brush of setae on distal one-third. Front tarsus of male (Figs.241 - 243) with basal three (in adults of few taxa all five) tarsomeres laterally expanded, with pads of adhesive setae (Figs.241 - 243) ventrally on basal two or three tarsomeres (pads rarely in area or entirely absent in adults of few taxa); females with all articles slender (also slightly laterally expanded in adults of few species), without pads. Middle and hind tarsi of both sexes slender in most adults (laterally expanded in few), slightly convex ventrally (adults with all tarsomeres expanded also have them ventrally concave (excavate)). Hind tarsus glabrous to sparsely pubescent dorsally, tarsomeres cylindrical (laterally compressed in few adults); fourth tarsomere (Figs.249 - 252) apically truncate (with ventro-apical setae symmetrical in length and number) or ventro-laterally extended as a short to moderately long lobe (with lateral ventro-apical setae longer and more numerous than medial setae and positioned on the extended lobe). Tarsal claws simple,

slender, evenly arcuate, equal in length.

Abdomen. All sterna with lateral pair of broad, faintly to markedly defined pits (Fig. 253), dorsolaterally carinate, but not otherwise modified as receptor or lock for elytra. Second visible sternum glabrous medially or (in few adults) with one or more scattered setae or sparse to dense patch of setae between hind coxae. Third to fifth visible sterna (Figs. 253 - 258) with one to eight posterior paramedial setae and zero to 15 anterior paralateral setae each side. Sixth visible (or "anal") sternum with one to four posterior paramedial setae (some species sexually dimorphic in number of setae) and no anterior paralateral setae each side.

Male genitalia. Median lobe tubular, complete, enlarged basally, with well-developed internal sac; basal bulb (Figs. 262 - 264) shape varied, globose, rounded and partially closed (basal orifice small, ventrobasal only) to quadrate or wedge-shaped and broadly open (basal orifice large); 'mid-shaft' (see section 3.217 above) (Figs. 262 - 287) very slender to very thick (lateral aspect), circular to laterally compressed in cross-section, cylindrical or tapered (apically or basally), axis markedly, arcuately bent (angle varied, from 90° to 140°), with or without right lateral pouch (Figs. 277 - 280) (slightly to markedly invaginated) or groove (Fig. 272); 'preapical-shaft' (lateral aspect) very long, slender (ventral and dorsal margins almost parallel, with apical orifice broadly open dorsally)to broad, short, (ventral and dorsal margins convergent apically at markedly acute to almost right angles, apical orifice broadly to narrowly open dorsally, dorsoapically or dorsal and right laterally), ventral margin (inner

curvature) straight to markedly recurved dorsally; apex varied in length, symmetry and shape (in dorsal, lateral, and apical aspects); internal sac varied in shape, uni- to multi-lobate, without plates, spines, setae or a flagellum (but with microtrichial fields). 'Dorsobasal sclerite' (Figs. 262 - 264) shape varied (entire, mid-dorsal and fin-like or from slightly to broadly split longitudinally, variously fused with or overlapping basal bulb). Parameres asymmetrical (symmetrical in length and shape in males of very few taxa); left paramere short, broad (in few males more elongate and/or narrowed), spatulate or apically narrowed and pointed; right paramere long, slender (in few males short and broad), arcuate, similar in curvature and length to median lobe, with or without a slender, strap-like sclerite ('right medial parameric' sclerite) (Figs. 292, 296) in medial membrane.

Female genitalia. Eighth abdominal sternum (Figs. 300 - 304) divided at middle in form of two hemisterna, each without vestiture except for row of sparse to dense setae on medial one-third of apical margin; basal apodeme moderate in width and length, apically truncate (Fig. 301) or emarginate (in some females very deeply) at middle in form of two distinct heads (with length of lateral head equal to (Fig. 302) or shorter than (Fig. 304) medial head, with lateral head vestigial in few females (Fig. 300)), without longitudinal reinforcing ridge (Figs. 300 - 304). Proctiger heavily sclerotized, shape varied (short, transverse, truncate apically (Fig. 305) to moderately long, hemispheric (Fig. 306)), glabrous. Paraprocts moderately to heavily sclerotized, shape triangular (Fig. 305), glabrous, narrowly to

broadly fused laterobasally with valvifer. Valvifer approximately triangular (Figs. 307 - 311), basal region heavily sclerotized, apicomedial region not to moderately sclerotized (if sclerotized, then not to broadly separated from basal region by membraneous area), with or without scattered setae in apicomedial region; basal apodeme lobate, length moderate (rarely shortened), positioned laterally. Vestige of tenth sternum split medially, each lateral piece pointed, lobate, fused with (or separate from but closely approximated to) medial angle of coxostylus (Figs. 312 - 313). Coxite and stylus fused medially in form of coxostylus, but apparently distinct laterally, ventrally and dorsally (separated by membraneous areas). Stylus region simple, non-segmented, without accessory lobes or teeth, produced apically as slightly to markedly arcuate blade; blade varied in length and shape, dorsolateral surface concave, ventromedial surface convex with one bisetiferous (in few females uni-or trisetiferous) subapical pore (pore absent only from N. complanata females), pore size varied, setae long; medial surface glabrous or sparsely to densely setose basally, medio-dorsal ridge glabrous or with one to six slender or spiniform setae. Coxite region membranous mid-laterally and ventrally to diagonal sclerotized margin, with row of one to 10 slender or spiniform setae (few females without setae) on or near diagonal margin (Figs. 315 - 321), medial surface glabrous or sparsely to densely setose apically. Bursa copulatrix with longitudinal axis varied, 'spermathecal chamber' slightly deflected dorsally (Fig. 315) to sigmoid (Fig. 328) or posterodorsally recurved (Fig. 327); 'vestibular chamber' (Fig. 322) broad, symmetrical, bell-shaped, slightly to markedly flared anterolaterally, dorsal wall

membranous (medially or paramedially sclerotized in few females), anterior wall in form of transverse septum between spermathecal chamber and common oviduct, medially with longitudinal reinforcement rod extended anteriorly in both spermathecal chamber and oviduct; spermathecal chamber shape varied (Figs. 324 - 343), width less than or equal to width vestibular chamber at their juncture, flat to vaulted, elongate-tubular-pointed anteriorly to short-broad-truncate anteriorly, symmetrical or anteriorly deflected left or right, main chamber in females of few taxa with accessory dorsal (Fig. 335) or ventral (Fig. 340) lobes, with or without sclerites (if present, sclerites associated with orifice of spermathecal duct in most females, present and not so associated in only few, shape varied), medial longitudinal reinforcement rod in ventral wall not sclerotized, in few females extended anteriorly as a narrow plate. Spermathecal duct (Figs. 345 - 352) very slightly sclerotized, varied in length (long to very short), diameter (narrow to thick throughout or thick only proximally), and shape (straight to irregular, sinusoidal or helical), point of insertion on spermathecal chamber varied (anterior, dorsal or posterior surface, medial or lateral position). Spermathecal gland absent. Spermatheca very slightly sclerotized, sac-like, shape (Figs. 345 - 352) varied (straight-tubular to ovoid or arcuate-lanceolate). Common oviduct membranous, without sclerites; medial longitudinal reinforcement rod in dorsal wall.

<u>Sexual dimorphism</u>.--In addition to primary sex differences between male and female reproductive systems (including genitalia), there is sexual dimorphism in several other characters among <u>Nebria</u> species.

Females of all but a few species (e.g. N. ingens) are larger than conspecific males; but, in most species, males have relatively larger eyes and longer antennae and legs than females. At least basal tarsomeres of front legs of males are laterally expanded and bear pads of adhesive hairs ventrally. These tarsomeres are slender and without pads in females. Females of most species have two or more pairs of "anal" setae (i.e. posterior paramedial setae on the sixth (last) visible sternum), and males of most species have only one pair.

Sexual dimorphism is also exhibited in one or more other characters by members of one or more Nebria taxa. These characters include: (1) development of elytral reflection (e.g. N. sahlbergii) (2) relative size or width of head (e.g. N. crassicornis or N. ingens); (3) relative width of pronotum (e.g. N. fuscipes Fuss, Palaearctic species); (4) relative length of elytra (e.g. N. ingens); and (5) elytral microsculpture, including depth of impression and shape of alveolae (e.g. N. arkansana) [see species descriptions, section 3.43 for details].

Geographical distribution.--Combined ranges of the several hundred species embraced by the present genus concept almost completely cover the Holarctic Region: Europe and Asia, north to the Arctic coast and southern Arctic islands, south to Taiwan, south slope of the Himalaya Mountains, Syria and Lebanon, west to Iceland, east to Asiatic Beringian islands, North Africa, north of the Sahara Desert, Morocco to Algeria. In the Nearctic Region, combined ranges of the 42 indigenous and one introduced species extend from the Arctic coast and Baffin Island south in mountainous areas to southern California, Arizona,

New Mexico and South Carolina; from North American Beringian islands east to Newfoundland; absent from the central and southern Great Plains and the southern and southeastern Coastal Plain.

Geographical relations with allied genera.--The other genera included in supertribe Nebriitae are generally sympatric with respect to Nebria. The ranges of Leistus, Pelophila, Opisthius and Paropisthius are completely within the geographical limits of Nebria, the last three genera occupying more restricted areas. The range of Notiophilus extends outside that of Nebria only in the southwestern Nearctic and northern Neotropical Regions where its populations reach the highlands of northern Guatemala.

Habitat distribution.--Members of this genus occupy a wide range of habitats in geographical areas with cold to cool-temperate climate and very few habitats (only those which offer cool microclimate) in warmer regions. Most species are markedly hydrophilous, with members living only at the margins of streams, lakes, snowfields or glaciers. A few species are independent of water bodies, with members in forests or in open woodlands and fields; populations of two species inhabit coastal sand dunes and open beaches; and those of one species are restricted to subterranean grottos and caves.

The genus is best represented in mountainous regions. Species exhibit a cumulative altitudinal range extending from sea level to the lower limits of permanent snow. Individual species generally occupy limited altitudinal ranges; and in areas with a diverse Nebria fauna and considerable topographic relief, striking and complex patterns of altitudinal zonation are evident (for details refer to section 4.22).

Dispersal potential.--A high percentage of species have members with reduced hindwings which cannot support flight. Adults with full-sized hindwings are probably capable of at least short-range flight; but, in general, dispersal is by means of ambulatory activity and the dispersive range of individuals is limited (see section 3.235). Dispersal of most taxa is, therefore, limited by relatively narrow zones of unsuitable habitat.

Natural history.--The beetles are nocturnal, opportunistic predator-scavengers, apparently feeding on any fresh (usually invertebrate) prey. They hide under stones or other cover in suitable habitats during the day. Timing of the life cycle, in all species studied, conforms to one of two patterns: a spring or an autumn breeding pattern. The larval stage consists of three instars. [Refer to section 3.23 for more extensive discussion of natural history.]

Fossil record.--Unquestionable representation of the genus in the fossil record is at present confined to samples of Late Tertiary (?Pliocene) and Quaternary age from Eurasia and North America. Few species have been recognized and fragments appear to be indistinguishable from comparable parts of members of extant species (see section 3.24).

3.42 Identification of Nearctic Nebria

3.421 Notes on the key and its use

As Simpson (1969:276) stated, the purpose of a key is to "facilitate identification of a specimen". Consequently, the characters a taxonomist uses in his efforts to distinguish and classify biological species are useful in a key only to the extent that they apply to all individuals. Because at least some variation (including sexual dimorphism) in many characters is common to almost all taxa, important taxonomic characters may be useless as key characters. Conversely, apparently trivial characters may be used in a key if they permit simple, rapid and reliable identification. Unfortunately, groups of two or more cryptic species (Smith, 1958) occur in nature, confounding identification by any but more sophisticated means. When differentiation in structural and distributional characters is negligible, there are essentially no good key characters. In such instances, the inability to identify individuals reflects an evolutionary reality (minimal differentiation or convergence) rather than some doubt as to the distinctiveness of the taxa.

Nearctic Nebria species and subspecies vary in the phenetic distinctiveness of their members and therefore in the ease with which individuals can be identified. Where possible, characters used in the key conform to the following criteria: (1) Universality: the state of the character is constant for all individuals of each taxon. Characters unique to one sex are avoided unless some character for the opposite sex is included in the couplet. Characters which are highly varied

within one taxon are not used unless the range of variation is essentially non-overlapping with that of the other taxon. (2) Accessibility: ease with which the state of a character is determined. Characters which can be studied only through dissection or which involve data not normally associated with a specimen are avoided if possible. Unfortunately, study of some important taxonomic and (occasionally) key characters (including development of the hindwings and structure of male and female genitalia) requires delicate dissection. Exclusion of genitalic characters prevents, for example, construction of a useful key to the Nearctic species groups because they require polythetic definition involving these characters. (3) Efficiency: speed of identification permitted by use of the character. Characters which are most evident, especially those which do not require use of a microscope (e.g. distributional characters) facilitate rapid progress through a key to an identification.

Organization of individual couplets is such that the most useful character is mentioned first, followed by supplementary characters which should reinforce the reader's initial choice between alternatives. The key assumes familiarity with structure and associated terms or carabid beetles; a few terms are used that are new. However, reference to appropriate discussions in section 3.2 and to the figures suggested in the key provides useful background and explanation. Particular difficulty may be encountered in couplets involving the following characters: form and depth of impression of microsculpture; continuity of elytral intervals (presence or absence of catenations); and absence or presence and intensity of metallic reflection. Preliminary reference

to discussions of these characters is almost essential to effective use of the key.

Extensive use of distributional characters in this key is justified by their efficiency and accessibility. Specimens without associated locality data are, fortunately, rare and seldom worth identifying; and the geographical distributions of most taxa are relatively well known. In two instances (namely, in couplets 64. and 65.), entries contain predictions on the probable occurrence of taxa where they are not yet known to occur (see appropriate species descriptions for present known ranges). Access to a comprehensive geographical atlas on North America is helpful to those without detailed knowledge of the continent.

At a few couplets in the key, dissections are required or suggested. For recommended dissection techniques, refer to section 2.22.

3.422 A Key for Identification of Adults of Nearctic Species and Subspecies of Nebria

i Front tarsus with basal three or four articles dilated, laterally expanded, with pads of adhesive setae ventrally on basal two or three articles .... MALE 1

i' Front tarsus with all articles slender (no broader than articles of middle or hind tarsus), without pads of adhesive setae ventrally .... FEMALE 1

1 (i,i') Midlateral pronotal seta present (Fig. 84) 2

1' Midlateral pronotal seta absent (Fig. 94) 46

2 (1) Head uniformly dark (dark rufous to black) 3

2' Head dark or pale; if dark, then vertex with one pair of pale paramedial spots (or pair fused to form a single median spot (Figs. 4 - 6) 16

3 (2) Metepisternum markedly punctate (Fig. 215); tarsomeres of hind tarsus sparsely pubescent dorsally (Fig. 247) [repeatedly introduced, but not established in Nearctic Region] .... N. brevicollis (Fabricius) (p. 341)

3' Metepisternum impunctate (Fig. 216); tarsomeres of hind tarsus glabrous dorsally (Fig. 248) 4

4 (3') Pronotum semiovoid (Fig. 84), basal sinuation of lateral margin absent or very short and shallow; fourth tarsomere of hind tarsus truncate ventrally (Fig. 249) with medial and

lateral apicoventral setae symmetrical in length and position; labium with paraglossae distinct as short, pointed apicolateral lobes on ligula (Fig. 61) .... *N. virescens* Horn (p. 345)

4' Pronotum distinctly cordate (Figs. 86 - 122), basal sinuation of lateral margin moderately to very deep; fourth tarsomere of hind tarsus not truncate (ventrolaterally extended as short to moderately long lobe (Figs. 250 - 252) with lateral apicoventral setae longer than medial setae and displaced toward apex of lobe); labium (Fig. 62) with paraglossae indistinct, fused with ligula 5

5 (4') Pronotum with small, longitudinal tubercle medial to midlateral seta (Fig. 89); fifth elytral interval with one to four setae 6

5' Pronotum without small, longitudinal tubercle medial to midlateral seta; fifth elytral interval without setae (rare individuals with single seta) 7

6 (5) Specimen from Alaska or northern Canada, east to west side of Ungava Bay, Quebec (or on Baffin Island). If locality in Quebec, elytra short, pronotum (Fig. 89) short and broad with basal sinuation of lateral margin moderately deep .... *N. nivalis nivalis* (Paykull) (p. 362)

6' Specimen from northeastern United States or Canada, from Maine (Mount Katahdin) to east side of Ungava Bay (or on Island of Newfoundland). If locality in Quebec, elytra long, pronotum (Fig. 90) long, narrowed basally with basal

sinuation of lateral margin very deep ....
.... N. nivalis gaspesiana new subspecies (p. 365)

7 (5') Second visible sternum with patch of setae medially (between hind coxae); third to fifth visible sterna each with two to six pairs of posterior paramedial setae 8

7' Second visible sternum glabrous medially; third to fifth visible sterna each with single pair of posterior paramedial setae 9

8 (7) Hind coxa unisetose basally; antennal scape (Figs. 25a, 25b) long, arcuate to bisinuate, narrow basally, broadly truncate apically; elytra slightly dull to moderately shiny, microsculpture moderately impressed, meshes slightly to moderately transverse and irregular; legs dark ....
.... N. hudsonica LeConte (p. 357)

8' Hind coxa bi- or trisetose basally; antennal scape (Fig. 24) moderately long, symmetrically ellipsoid; elytra dull, microsculpture very deeply impressed, meshes isodiametric to very slightly transverse; legs dark or pale ....
.... N. gouleti new species (p. 356)

9 (7') Elytra very shiny (or faintly iridescent), microsculpture of thin, transverse lines without (or with only a few scattered) meshes, intervals markedly convex, striae very deeply impressed; pronotum (Figs. 87 - 88) with apical angles very broad, basal angles slightly to moderately obtuse 10

9' Elytra dull to slightly shiny, microsculpture of isodiametric to moderately transverse meshes, intervals flat to

moderately convex, striae moderately deeply impressed; pronotum (Figs. 92 - 93) with apical angles narrow to moderately broad, basal angles rectangular to acute 11

10 (9) Specimen from eastern North America north of French Broad River (North Carolina) (Fig. 384) .... N. lacustris lacustris Casey (p. 358)

10' Specimen from southeastern United States, south of French Broad River (Fig. 384) .... N. lacustris bellorum new subspecies (p. 359)

11 (9') Head, pronotum and elytra brassy to brilliant metallic green; or, if non-metallic dorsally, pronotal microsculpture very deeply impressed, meshes isodiametric, alveolae slightly convex; penultimate labial palpomere bisetose (trisetose only in very few individuals); third elytral interval clearly catenate (setiferous pores broadly foveate) .... N. frigida R. F. Sahlberg (p. 375)

11' Head, pronotum and elytra non-metallic; pronotal microsculpture faintly to deeply impressed, meshes isodiametric, alveolae flat; penultimate labial palpomere trisetose; third elytral interval continuous or faintly catenate (setiferous pores weakly to moderately foveate) 12

12 (11') Pronotum (Figs. 92 - 93) large, broad, markedly cordate (lateral margin markedly arcuate at middle), dull, microsculpture deeply impressed, meshes isodiametric; head (Figs. 13 - 14) large, very convex, with genae and occiput

broad and eyes slightly reduced in size 13

12' Pronotum (Figs. 93A, 93B) small, slightly narrow, moderately cordate (lateral margin moderately arcuate at middle), slightly dull to moderately shiny, microsculpture moderately to faintly impressed, meshes isodiametric; head (Fig. 14A) moderate in size and convexity, with genae and occiput not broadened and eyes full-sized 14

13 (12) Specimen from the Olympic Peninsula or Cascade Range and adjoining ranges of southwestern British Columbia to central Washington (Fig. 387). Head (Fig. 13) with microsculpture faintly impressed, meshes isodiametric, genae and occiput very broad; pronotum (Fig. 92) markedly narrowed basally, apical angles markedly projected anteriorly, narrowed and bluntly pointed apically .... N. crassicornis crassicornis Van Dyke (p. 366)

13' Specimen from east of the Columbia Basin in Oregon or Washington, east of the Okanagan Valley in southern British Columbia, or in northern British Columbia south to Terrace (Fig. 387). Head (Fig. 14) with microsculpture moderately impressed, meshes isodiametric, genae and occiput moderately broad; pronotum (Fig. 93) moderately narrowed basally, apical angles moderately projected anteriorly, slightly narrowed, rounded .... N. crassicornis intermedia Van Dyke (p. 367)

14 (12') Antennal scape (Figs. 27a, 27b) short, straight, symmetrically ovoid or anteriorly more convex; hindwing

full-sized. Specimen from northern Sierra Nevada of California or the Cascade Range of Oregon (south of Columbia River) (Fig. 388) .... _N. gyllenhali lassenensis_ new subspecies (p. 374)

14' Antennal scape (Figs. 26, 28) long, straight to slightly arcuate, markedly to moderately narrowed basally; hindwing full or reduced in size and venation pattern. Specimen from north or east of above area (Fig. 388) 15

15 (14') Hindwing (Fig. 192) reduced in length, width and venation. Specimen from southern Rocky Mountains, in Medicine Bow Range or more southerly ranges (Fig. 388) .... _N. gyllenhali lindrothi_ new subspecies (p. 374)

15' Hindwing (Fig. 191) full-sized. Specimen from more northern area of Rocky Mountain region (south to Laramie Mountains) or from area northeast or northwest (Fig. 388) .... _N. gyllenhali castanipes_ Kirby (p. 369)

16 (2') Basolateral pronotal seta absent (Fig. 111)............. 17

16' Basolateral pronotal seta present (Fig. 113) 19

17 (16) Specimen from east of Columbia Basin of Washington and Oregon. Penultimate labial palpomere bisetose; mentum (Fig. 72) with M_1 setae absent .... _N. carri_ new species (p. 413)

17' Specimen from Cascade Range or area further west. Penultimate labial palpomere trisetose; mentum (Fig. 73) with M_1 setae present 18

18 (17') Basal margination of elytron (Fig. 149) very short and wavy, markedly concave. Specimen from Olympic Peninsula, Vancouver Island, or on mainland from Cascade Range of northern Washington or Coast Ranges from southern British Columbia to southeastern Alaska (Fig. 405) .... N. kincaidi kincaidi Schwarz (p. 414)

18' Basal margination of elytron (Fig. 150) moderately long, smooth (or faintly wavy), slightly to moderately concave. Specimen from Cascade Range of central Washington to northern Oregon (Fig. 405) .... N. kincaidi balli new subspecies (p. 415)

19 (16') Specimen from California, extreme western Nevada or extreme southwestern Oregon 20

19' Specimen not from California, western Nevada or southwestern Oregon 28

20 (19) Elytra clearly with moderate to faint metallic (violet, blue or green) reflection 21

20' Elytra without metallic reflection 23

21 (20) Size very large: standardized body length male greater than 12.5 mm, female greater than 11.3 mm; elytral silhouette (Fig. 139) markedly ovoid, narrowed basally .... N. ingens riversi Van Dyke (p. 425)

21' Size moderate: standardized body length male less than 12.0 mm, female 12.3 mm to 9.5 mm; elytral silhouette (Fig. 136) subrectangular, broad basally 22

22 (21') Specimen from southern Sierra Nevada (Fig. 406). Pronotum (Fig. 114) markedly cordate, basal angles acute, projected posteriorly; basal elytral margination (Fig. 152) straight to slightly concave ....
.... N. meanyi lamarckensis new subspecies (p. 420)

22' Specimen from Cascade Range (at present known only from Mount Shasta in California). Pronotum (Fig. 113) moderately cordate, basal angles rectangular, denticulate posteriorly; basal elytral margination (Fig. 151) slightly to moderately concave ..... N. meanyi meanyi Van Dyke [in part] (p. 419)

23 (20') Elytral silhouette (Figs. 136 - 137) subrectangular to subovoid; hindwing full-size 24

23' Elytral silhouette markedly ovoid, narrowed basally; hindwing vestigial 25

24 (23) Specimen from Klamath Mountain System of Coast Ranges in northwestern California or southwestern Oregon. Apical angles of pronotum (Fig. 110) moderately narrow; elytral silhouette (Fig. 137) subovoid, relatively short and broad
.... N. gebleri siskiyouensis new subspecies (p. 412)

24' Specimen from Sierra Nevada or extreme southern Cascade Range. Apical angles of pronotum (Fig. 109) moderately broad to slightly narrow; elytral silhouette (Fig. 136) subrectangular, relatively long and narrow ....
.... N. gebleri rathvoni LeConte (p. 411)

25 (23') Size very large: standardized body length male greater than 12.5 mm, female greater than 12.0 mm; elytra black,

moderately shiny, with microsculpture faintly impressed, meshes isodiametric (often broken) .... N. ingens ingens Horn (p. 424)

25' Size moderate: standardized body length male less than 12.0 mm, female less than 12.4 mm; elytra rufous to piceus, very dull, with microsculpture deeply impressed, meshes isodiametric 26

26 (25') Head (Fig. 19) with genae and occiput swollen, very broad, eyes slightly reduced in diameter and convexity, antennal scape (Figs. 33a, 33b) ovoid, symmetrical to more convex anteriorly .... N. ovipennis LeConte (p. 417)

26' Head (Fig. 20) with genae and occiput not swollen, eyes average in size and convexity, antennal scape (Figs. 34 - 35) cylindrical or narrowed basally and apically truncate 27

27 (26') Antennal scape (Fig. 35) short, straight, cylindrical. Specimen from Great Western Divide (southern Sierra Nevada) (Fig. 403)....... N. spatulata spatulata Van Dyke (p. 416)

27' Antennal scape (Fig. 35) medium length, slightly arcuate, markedly narrowed basally. Specimen from Eastern Divide or more northern Sierra Nevada (Fig. 403) .... N. spatulata sierrae new subspecies (p. 417)

28 (19') Elytral silhouette (Figs. 139, 145) markedly ovoid 29

28' Elytral silhouette subovoid to subrectangular 31

29 (28) Elytra clearly with faint to moderate metallic (violet) reflection; size moderate: standardized body length male

less than 11.5 mm, female less than 12.0 mm .... N. paradisi Darlington (p. 354)

29' Elytra without metallic reflection; size very large: standardized body length male greater than 12.0 mm, female greater than 12.5 mm 30

30 (29') Antennal scape (Fig. 36) cylindrical, straight. Specimen from Olympic Range or Cascade Range north of Columbia River .... N. vandykei vandykei Bänninger (p. 425)

30' Antennal scape (Fig. 37) narrowed basally, straight or slightly arcuate. Specimen from Cascade Range south of Columbia River .... N. vandykei wyeast new subspecies (p. 426)

31 (28') Head (Fig. 21) large, broad; pronotum (Fig. 116) markedly cordate, broad; elytra with silhouette rectangular to subrectangular, broad, with marked metallic (violet, brassy, or green) reflection, intervals moderately to markedly convex .... N. metallica Fischer v. Waldheim (p. 421)

31' Combination of character states not as above. If head slightly large and broad (for average proportions see Fig. 18), then pronotum moderately cordate; elytra with silhouette subovoid, without or with only faint metallic reflection, intervals flat to moderately convex 32

32 (31') Specimen from locality in Rocky Mountain Region: south of Peace River (British Columbia), east of Fraser Plateau and Okanagan Valley (British Columbia), east of Columbia Basin and Great Basin 33

32' Specimen from locality northwest or west of above area 42

33 (32) Elytra with marked metallic (violet, blue or green) reflection 34

33' Elytra without or with very faint metallic reflection 38

34 (33) Specimen from Colorado or New Mexico. Pronotum (Fig. 120A) narrow; elytral silhouette (Fig. 138) narrowed basally, lateral margins almost straight posterior to humeral angles .... _N. purpurata_ LeConte (p. 429)

34' Specimen from north or northeast of Colorado. Pronotum broad; elytral silhouette subrectangular, broad basally 35

35 (34') Size moderate: standardized body length male less than 10.5 mm, female less than 11.0 mm, pronotum (Figs. 107, 110A) moderately cordate, narrowed basally 36

35' Size very large: standardized body length male greater than 12.0 mm, female greater than 12.5 mm; pronotum (Figs. 119 - 120) slightly cordate, broad basally 37

36 (35) Specimen from Strawberry Range of Blue Mountains, eastern Oregon (Fig. 402). Elytra with green metallic reflection; apex median lobe of male as in Fig. 276 ; bursa copulatrix with anteroventral sclerite (Fig. 334) .... _N. gebleri strawberriensis_ new subspecies (p. 413)

36' Specimen not from Strawberry Range. Elytra with violet (in few adults blue or green) metallic reflection; apex median

lobe of male as in Fig. 275 ; bursa copulatrix without anteroventral sclerite (Fig. 333) .... N. gebleri gebleri Dejean [in part] (p. 408)

37 (35') Specimen from Alberta or British Columbia. Pronotum (Fig. 119) moderately convex, slightly narrowed basally; hind coxa (Fig. 226) with two to five basal and two to six apical setae .... N. schwarzi schwarzi Van Dyke (p. 428)

37' Specimen from Wyoming. Pronotum (Fig. 120) slightly convex to slightly flattened, broad basally; hind coxa (Fig. 227) with four to six basal and usually one (rarely two or three) apical seta .... N. schwarzi beverlianna new subspecies (p. 428)

38 (33') Specimen from Tushar Mountains or Midget Crest, southwestern Utah (Fig. 410). Antennal scape (Fig. 41) arcuate, markedly narrowed basally; elytra with faint metallic violet or blue reflection; apex median lobe of male as in Fig. 285 ; bursa copulatrix with posterodorsal sclerite as in Fig. 336A .... N. piute Erwin and Ball (p. 433)

38' Specimen not from Tushar Mountains or Midget Crest. Antennal scape (Figs. 38 - 40) slightly arcuate or straight, markedly to slightly narrowed basally; elytra with or without faint metallic reflection 39

39 (38') Pronotum (Fig. 122) with basal sinuation of lateral margin very deep; elytra with faint metallic violet reflection, microsculpture faintly to moderately impressed, meshes isodiametric or broken; apex median lobe of male as in Fig.

284 , apical orifice broad, markedly oblique; bursa copulatrix with posterodorsal sclerite as in Fig. 336 . Specimen from central or northwestern Colorado (Fig. 410) .... *N. coloradensis* Van Dyke (p. 432)

39' Pronotum (Figs. 121, 121A) with basal sinuation of lateral margin moderately deep; elytra without (or in few adults with very faint) metallic reflection, microsculpture deeply impressed, meshes isodiametric; apex median lobe of male varied (Figs. 281 - 283), but if specimen from central or northern Colorado, then apical orifice narrow, only slightly oblique 40

40 (39') Specimen from Henry Mountains, southeastern Utah (Fig. 411). Hindwing (Fig. 196) reduced in width and length, truncate distal to stigma; apex median lobe of male as in Fig. 283 ; bursa copulatrix with posterodorsal sclerite as in Fig. 339 .... *N. trifaria utahensis* new subspecies (p. 432)

40' Specimen not from Henry Mountains. Hindwing width and length varied 41

41 (40') Specimen from southwestern Colorado, New Mexico, or southeastern Utah (Fig. 411). Antennal scape straight; each epilobe of mentum (Fig. 78) with apical tooth moderately long; elytra with or without very faint metallic violet reflection, intervals moderately convex; apex median lobe of male (Fig. 282) elongate, arcuate; bursa copulatrix as in Fig. 338. .... *N. trifaria catenata* Casey (p. 431)

41' Specimen not from above area (Fig. 411). Antennal scape

slightly to moderately arcuate; each epilobe of mentum (Fig. 77) with apical tooth minute; elytra without metallic reflection, intervals flat to slightly convex; apex median lobe of male (Fig. 281) short, bent but not arcuate; bursa copulatrix varied (Figs. 337a-337d) .... N. trifaria trifaria LeConte (p. 430)

42 (32') Elytra (Fig. 144) flat to slightly convex, broad basally, humeral angles smoothly, roundly rectangular, humeral carinae absent; pronotum (Fig. 118) with basal sinuation of lateral margin shallow .... N. piperi Van Dyke (p. 427)

42' Elytra moderately convex, moderately broad basally, humeral angles faintly to moderately obtuse, humeral carinae present, slightly to markedly developed; pronotum (Figs. 108, 113) with basal sinuation of lateral margin moderately to very deep 43

43 (42') Fifth elytral interval with three to six setae, markedly catenate, striae deeply impressed 44

43' Fifth elytral interval without setae (rarely with one to three setae), not (in few specimens moderately) catenate, striae moderately impressed 45

44 (43) Specimen from Olympic Peninsula, Washington, or Vancouver Island, British Columbia, (Fig. 406). Pronotum (Fig. 115) markedly cordate, basal sinuation of lateral margin very short and deep; elytron with basal margination slightly short, intervals markedly convex .... N. meanyi sylvatica new subspecies (p. 420)

44' Specimen from Cascade Range of Oregon, Washington, or southern British Columbia, or from Coast Ranges of mainland British Columbia or southeastern Alaska (Fig. 406). Pronotum (Fig. 113) moderately cordate, basal sinuation of lateral margin moderately long and deep; elytron with basal margination long, intervals moderately convex .... _N. meanyi meanyi_ Van Dyke [in part] (p. 419)

45 (43') Specimen from Cascade Range of central Oregon to southern British Columbia (Fig. 402). Pronotum (Fig. 108) markedly cordate, basal sinuation of lateral margin very deep; elytral silhouette subovoid, slightly narrowed basally, basal margination moderately concave, humeral angles roundly obtuse, humeral carinae moderately to markedly developed .... _N. gebleri cascadensis_ new subspecies (p. 410)

45' Specimen from north or east of above area (Fig. 402). Pronotum (Fig. 107) moderately cordate, basal sinuation of lateral margin moderately deep; elytral silhouette subrectangular, moderately broad basally, basal margination straight to slightly concave, humeral angles faintly and roundly obtuse, humeral carinae absent or slightly developed .... _N. gebleri gebleri_ Dejean [in part] (p. 408)

46 (1') Hind coxa (Fig. 228) unisetose basally; third to fifth visible abdominal sterna (Fig. 257) each with single pair of posterior paramedial setae (in very few specimens bisetose unilaterally on one sternum); middle tibia (Fig. 237) dorsally flat to slightly convex throughout, brush of dorsal

setae slightly to moderately developed 47

46' Hind coxa (Fig. 229) bi- or plurisetose basally; third to fifth visible abdominal sterna (Fig. 258) each with two or more pairs of posterior paramedial setae (in very few specimens unisetose unilaterally on one sternum); middle tibia (Figs. 238 - 240) dorsally concave to deeply sulcate (at least near middle, in many specimens also toward apex), brush of dorsal setae moderately to markedly and densely developed 48

47 (46) Size very small: standardized body length male 8.2 mm or less, female 8.8 mm or less; pronotum (Fig. 102) with basal sinuation of lateral margin short, deep, lateral explanation narrow, basal angles rectangular; elytral microsculpture faintly impressed, meshes isodiametric to slightly transverse .... _N. appalachia_ Darlington (p. 396)

47' Size moderate: standardized body length male greater than 8.4 mm, female greater than 8.8 mm; pronotum (Fig. 103) with basal sinuation of lateral margin absent or shallow, lateral explanation very broad, basal angles obtuse; elytral microsculpture moderately impressed, meshes markedly transverse or in form of dense transverse lines without meshes .... _N. pallipes_ Say (p. 397)

48 (46') Pronotum (Figs.105 - 106) with basal angles obtuse, basal sinuation of lateral margin shallow or absent 49

48' Pronotum with basal angles clearly rectangular or acute, basal sinuation of lateral margin shallow to deep 52

49 (48) Elytral silhouette (Fig. 142) ovoid; color body and appendages entirely pale yellow to orange-tan. Specimen from south-central Utah .... N. desolata Kavanaugh [in part] (p. 402)

49' Elytral silhouette subovoid to subrectangular; if subovoid, then body color and appendages darker (dark rufous to piceus) 50

50 (49') Elytral silhouette (Fig. 137) subovoid, lateral margins clearly rounded; tooth of mentum (Fig. 70) bifid, with notch flat medially; lateral explanation of pronotum (Fig. 105) narrow at middle, broadened apically and basally .... N. mannerheimii Fischer v. Waldheim (p. 400)

50' Elytral silhouette (Figs. 136 - 137) subrectangular, lateral margins faintly rounded or straight (even when elytra narrowed basally); tooth of mentum (Fig. 69) bifid with notch simply V-shaped; lateral explanation of pronotum (Figs. 100 - 101) broadened posteriorly only 51

51 (50') Mandible (Fig. 59) markedly explanate laterally, broad; pronotum (Fig. 101) slightly cordate, broad basally, widest anterior to middle, slightly shiny (microsculpture faintly to moderately impressed, meshes isodiametric), basal margin not or slightly sinuate laterally, lateral bead narrow, obliterated basally in most specimens, basal foveae broad, smooth to faintly rugulose ..... N. obliqua LeConte (p. 394)

51' Mandible (Fig. 58) moderately explanate laterally; pronotum (Figs. 100a,100b) moderately cordate, narrowed basally,

widest near middle, moderately dull (microsculpture moderately to deeply impressed, meshes isodiametric), basal margin markedly sinuate laterally, lateral bead wide, complete to base, basal foveae narrow, faintly punctulate .... _N. suturalis_ LeConte (p. 392)

52 (48') Elytral silhouette ovoid, markedly narrowed basally, humeral angles markedly rounded and obtuse 53

52' Elytral silhouette rectangular to subovoid, not or moderately narrowed basally, humeral angles not markedly rounded and obtuse 57

53 (52) Fifth and seventh elytral intervals with setiferous pores, slightly catenate (some individuals with setae absent unilaterally from fifth or seventh interval); body and appendages pale yellow. Specimen from sea coast locality, from northern California to central British Columbia (including Vancouver Island or Queen Charlotte Islands) .... _N. diversa_ LeConte (p. 405)

53' Fifth and seventh elytral intervals without setiferous pores (if a single seta present on seventh interval, then specimen from Sierra Nevada, eastern California); body color dark to pale. Specimen from interior locality, California or Utah 54

54 (53') Specimen from Sierra Nevada, California (Fig. 390). Antennal scape (Fig. 29) slightly arcuate, cylindrical; each epilobe of mentum (Fig. 66) with apical tooth very long; pronotum (Fig. 94) with lateral margin slightly

arcuate, sinuate subapically, lateral explanation narrow, slightly broadened apically.... _N. lyelli_ Van Dyke (p. 379)

54' Specimen from Utah. Antennal scape (Figs. 31 - 32) straight to arcuate, ovoid to narrowed basally and truncate apically; each epilobe of mentum (Fig. 71) with apical tooth moderately long; pronotum (Figs. 99, 106) with lateral margin moderately arcuate, not sinuate subapically, lateral explanation broad (or, if narrowed at middle, then broadened basally) 55

55 (54') Pronotum (Fig. 106) with basal sinuation of lateral margin short and shallow, lateral explanation narrow at middle, broadened basally, basal angles rectangular; elytra vaulted, moderately convex; body and appendages pale yellow to orange-tan .... _N. desolata_ [in part] (p. 402)

55' Pronotum (Fig. 99) with basal sinuation of lateral margin moderately long and deep, lateral explanation moderately and uniformly broad, basal angles rectangular to acute, projected posteriorly; elytra not vaulted, slightly flattened; body and appendages dark to pale 56

56 (55') Antennal scape (Fig. 32) medium length, straight, almost cylindrical, slightly narrowed basally; body and appendages dark (piceus to black). Specimen from Pine Valley Mountains (Fig. 394) .... _N. zioni oasis_ new subspecies (p. 391)

56' Antennal scape (Figs. 31a, 31b) long to medium, slightly arcuate, moderately narrowed basally; body and appendages

dark to pale. Specimen not from above area (Fig. 394)
.... N. zioni zioni Van Dyke (p. 390)

57 (52') Humeral carinae (Fig. 157) markedly developed and projected anterolaterally 58

57' Humeral carinae (Figs. 158a, 158b) absent to moderately developed, not or slightly projected anterodorsally 59

58 (57) Specimen from Olympic Peninsula (Fig. 390). Elytra slightly shiny, microsculpture moderately impressed, meshes isodiametric (broken) or slightly transverse; pronotum (Fig. 96) moderately cordate, basal sinuation of lateral margin moderately short and deep; apex median lobe of male as in Fig. 266 ; bursa copulatrix (Fig. 329) without anterodorsal sclerite .... N. acuta quileute new subspecies (p. 380)

58' Specimen from northern Sierra Nevada, Cascade Range from northern California to southern British Columbia, or from Coast Ranges of mainland from southern British Columbia to southeastern Alaska (Fig. 390). Elytra moderately dull, microsculpture moderately impressed, meshes isodiametric (unbroken); pronotum (Fig. 95) slightly cordate, basal sinuation of lateral margin moderately long and shallow; apex median lobe of male as in Fig. 265 ; bursa copulatrix (Fig. 328) with anterodorsal sclerite ....
.... N. acuta acuta Lindroth (p. 379)

59 (57') Pronotum (Figs. 104 - 106) with lateral explanation narrow at middle, broadened posteriorly 60

59' Pronotum (Figs. 97 - 98) with lateral explanation broad

throughout 62

60 (59) Legs dark brown to piceus, body black; microsculpture on pronotum and elytra very deeply impressed, meshes isodiametric, alveolae convex. Specimen from California (Fig. 399) .... _N. darlingtoni_ new species (p. 399)

60' Legs pale yellow, body dark (piceus) to pale (orange-tan); microsculpture on pronotum and elytra moderately impressed, meshes isodiametric, alveolae flat 61

61 (60') Specimen from Arizona (Fig. 400). Hindwing (Fig. 195) short, narrow; apex of fourth tarsomere of hind tarsus with ventrolateral lobe long; apex median lobe of male as in Fig. 273 .... _N. navajo_ new species (p. 402)

61' Specimen from Pacific Coast states, southern California to northern Washington, or inland from westcentral Idaho or extreme western Nevada (Fig. 400). Hindwing full-sized; apex of fourth tarsomere of hind tarsus with ventrolateral lobe short, only slightly developed; apex median lobe of male as in Fig. 274 .... _N. eschscholtzii_ Ménétriés (p. 403)

62 (59') Elytral silhouette (Figs. 141 - 142) subovoid AND specimen from Aleutian Islands, Alaska, or Queen Charlotte Islands, British Columbia (Fig. 393); head (Figs. 15 - 16) relatively large and broad 63

62' Elytral silhouette rectangular, subrectangular or subovoid (if subovoid, then specimen from the central or southern Rocky Mountain regions); head size and width average (see Fig. 18) 64

63 (62) Specimen from Aleutian Islands (Fig. 393). Eyes (Fig. 15) protruding, very convex; each epilobe of mentum (Fig. 67) with apical tooth moderately long; prosternal intercoxal process (Fig. 129) sublanceolate, unmargined at apex; elytra (Fig. 141) elongate, narrow, with faint metallic green reflection, humeral carinae slightly to moderately developed, slightly projected anterodorsally .... N. gregaria Fischer v. Waldheim (p. 385)

63' Specimen from Queen Charlotte Islands (Fig. 393). Convexity of eyes average (see Fig. 16); each epilobe of mentum (Fig. 68) with apical tooth minute; prosternal intercoxal process (Fig. 128) lanceolate, completely margined; elytra (Fig. 142) slightly shortened, moderately broad, without metallic reflection, humeral carinae absent .... N. charlottae Lindroth (p. 386)

64 (62') Specimen from northern California or extreme southern Oregon 65

64' Specimen from north or east of above area 66

65 (64) Specimen from Klamath Mountain System of the Coast Ranges, northwestern California or southwestern Oregon (Fig. 391). Pronotum (Fig. 98) large, broad, basal sinuation of lateral margin moderate in depth and length, basal angles rectangular, minutely denticulate; proepisternum smooth; elytra moderate in length and basal width, without metallic reflection .... N. sahlbergii triad new subspecies (p. 384)

65' Specimen from Warner Mountains, northeastern California or southcentral Oregon (Fig. 391). Pronotum (Fig. 97) size moderate, basal sinuation of lateral margin deep and long, basal angles rectangular, not denticulate; proepisternum faintly punctulate anteriorly; elytra slightly short and narrowed basally, in most specimens with very faint metallic green or violet reflection .... N. sahlbergii modoc new subspecies (p. 383)

66 (64') Hindwing with full reflexed tip (Fig. 182) or truncate (Fig. 193) distal to stigma; if truncate, then wing not also narrowed; elytral silhouette rectangular to subovoid 67

66' Hindwing reduced in length and width (Figs. 188, 194); if truncate, then wing also narrowed (Fig. 194); elytral silhouette subrectangular to subovoid 70

67 (66) Specimen from La Sal Mountains, Utah (Fig. 392). Elytral silhouette subrectangular; hindwing full-sized; apex median lobe of male as in Fig. 269; bursa copulatrix with posterodorsal sclerite as in Fig. 332 .... N. arkansana oowah new subspecies (p. 388)

67' Specimen not from above area. Hindwing full-sized or truncate distal to stigma 68

68 (67') Specimen from locality in eastern Southern Rocky Mountain Region (Fig. 392): northern New Mexico to southern Wyoming (Medicine Bow and Sierra Madre Ranges) or west in San Juan Mountains of Colorado or Abajo Mountains of southeastern Utah. Elytral silhouette subrectangular to subovoid,

basally narrowed; hindwing truncate distal to stigma or, if reflexed tip present, entire wing slightly miniature .... _N. arkansana arkansana_ Casey (p. 386)

68' Specimen from locality northwest (Fig. 392) of above area. Elytral silhouette rectangular to subrectangular, broad basally; hindwing full-sized or truncate distal to stigma (if truncate, specimen from Aleutian Islands, Alaska) 69

69 (68') Median lobe of male (Fig. 268) broad, with apex short and narrow; bursa copulatrix with posterodorsal sclerite as in Fig. 331 ; elytra slightly to moderately dull, microsculpture with meshes isodiametric to slightly transverse, basal margination (Fig. 147) straight to slightly concave, merged smoothly with lateral margination, humeral carinae absent or very slightly developed .... _N. arkansana edwardsi_ new subspecies (p. 387)

69' Median lobe of male (Fig. 267) narrow, with apex moderately long and broad, deflected ventrally; bursa copulatrix with posterodorsal sclerite as in Fig. 329A ; elytra slightly dull to shiny, microsculpture with meshes slightly to markedly transverse or in form of fine transverse lines without meshes, basal margination (Figs. 158a,158b) slightly to moderately concave, merged with lateral margin at obtuse angle, humeral carinae slightly to moderately developed .... _N. sahlbergii sahlbergii_ Fischer v. Waldheim (p. 381)

70 (66') Specimen from Uinta Mountains or Wasatch Mountains at or

north of Weber River, Utah (Fig. 392). Median lobe of male as in Fig. 270 .... _N_. _arkansana_ _uinta_ new subspecies (p. 389)

70' Specimen from north or south of above area (Fig. 394). Median lobe of male as in Fig. 271 71

71 (70') Specimen from Wasatch Mountains south of Weber River, Utah (Fig. 394). Elytra dull (microsculpture deeply impressed, meshes isodiametric), without metallic reflection .... _N_. _fragilis_ _fragilis_ Casey (p. 389)

71' Specimen from westcentral Wyoming (Fig. 394). Elytra slightly shiny (microsculpture faintly impressed, meshes irregular isodiametric to slightly transverse), with or without very faint metallic green or violet reflection .... _N_. _fragilis_ _teewinot_ new subspecies (p. 390)

3.43 Species groups, species, and subspecies

Because of time constraints on completion of this dissertation, I have greatly reduced the coverage and completeness of this section. Material included is intended as a sample of what will appear in the manuscript for publication. Nomenclatural treatment presented (including type designation, synonymies, and bibliographies on each species-group taxon) is complete, covering all Nearctic taxa. Informal synonymies and diagnoses are provided for each of the lineages and species groups represented in the Nearctic fauna. A complete descriptive treatment is provided only for the virescens lineage--this as an example of format and coverage intended for all taxa. All crucial descriptive data can be retrieved, however, from Fig. 372 used in concert with Table 15.

3.431 Introduced species

Apparently only one Nebria species has been introduced into North America--namely, Nebria brevicollis (Fabricius), type species of genus Nebria, native to western Europe, where its members abound in woodlands as well as in parks, gardens, and other synanthropic habitats. Two adults of this species have been collected in North America; but these records are widely separated in space (see Fig. 380) and time (see Appendix B, and Lindroth, 1961a). These adults undoubtedly represented two separate introductions, neither of which has apparently resulted in permanent colonization by this species. For completeness of coverage of the literature on Nebria in the Nearctic region, I offer the following brief nomenclatural treatment.

Nebria brevicollis (Fabricius)

(Figures 60, 125, 133-134, 213, 215, 233-235, 247, 263, 294, 353, 380)

Carabus brevicollis Fabricius, 1792:150. LECTOTYPE (designated by Lindroth, 1961a:78), a male, in ZMKD, labelled: "Lectotypus brevicollis F. design. Lth. 1961." [red label]. TYPE LOCALITY. --Germany.

Nebria brevicollis (Fabricius).--Larochelle, 1975:94.--Lindroth, 1954d:38; 1955a:42; 1961a:78 1963a:12.

Notes on nomenclature and types.--Because N. brevicollis is not a permanent member of the Nearctic fauna, I have listed above only those references which deal with its Nearctic occurrence. Numerous synonyms of (see Csiki, 1927:385; Larochelle, 1975:94) and over 100

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

literature references to N. brevicollis in the Palaearctic Region have been omitted.

3.432 The virescens lineage

This lineage is represented by only three extant species, two of which (N. chalceola Bates and N. pusilla Ueno) are restricted to Japan (Fig. 412). The third species is endemic to western North America. Included in this lineage are taxa previously assigned to Lindroth's (1961a) "virescens" group and genus Nipponebria Ueno (Habu, 1958).

Diagnostic combination.--Adult members of this lineage can be recognized by the following combination of character states: frontal red spot(s) absent; paraglossae distinct, but minute and dentiform; pronotum semiovoid (except slightly cordate in N. pusilla adults), midlateral pronotal setae present; hind coxa with one seta at base; ventroapical margin of fourth hind tarsomere truncate, not projected; second through fifth visible abdominal sterna without anterior paralateral setae; male genitalia: median lobe with basal bulb rounded, globose, partially closed basally, midshaft axis bent 135° or more, apex (ventral aspect) broad, shovel-shaped; dorsobasal piece distinct, in form of an expanded crest in dorsal midline (Fig. 262); female genitalia: basal apodeme of eighth sternum very deeply emarginate, lateral arm reduced to faint lobe or absent; proctiger transverse or hemispheric, membranous apically, heavily sclerotized

basally only; medial area of valvifer moderately sclerotized; coxite with setae of ventral diagonal row spiniform; stylus with setae of mediodorsal row medium length and spiniform (except long in _N. virescens_ females), mediodorsal row diagonal; bursa copulatrix without sclerite in dorsal wall of spermathecal chamber.

Sexual dimorphism.--As described for genus.

Geographical distribution.--The geographical range of this lineage is markedly disjunct--one species restricted to western North America, and two species restricted to Japan.

Geographical relations with allied taxa.--The geographical range of this lineage is broadly sympatric with the respective ranges of each of the other lineages represented in the Nearctic regions, and also with ranges of endemic Palaearctic lines.

Habitat distribution.--Collectively, members of this lineage occupy broad macro- and microhabitat ranges. However, the Palaearctic species are apparently more narrowly restricted than the Nearctic _N. virescens_ (see description below). _N. chalceola_ members live in moist forest habitats (e.g. in leaf litter or loose soil, under moss mats, etc.) (Habu, 1958) at relatively low altitudes. _N. pusilla_ members are restricted to high montane areas (2000 m level or above) (Habu, 1958), where they are found under stones.

Ecophenotypic variation.--See discussion for _N. virescens_ below.

Taxonomic notes.--It could be effectively argued at present that members of this lineage represent such a distinctive monophyletic unit that it should be recognized as a separate genus--as Habu (1958) has already suggested for the Palaearctic species alone (i.e. genus

Nippononebria). At present, however, pending a more complete review of Nebria and related genera on a worldwide basis, I prefer to emphasize relationships both among lineage members and between this lineage and the rest of genus Nebria by including all in a single genus.

Phylogenetic relationships.--If my cladistic analysis of relationships is correct, the virescens lineage represents the sister group of all other extant Nebria (in the broadest sense). However, members of this lineage share a discomforting number of characteristics with members of other nebriine genera, especially Leistus. Although shared character states may be symplesiotypic, alternate interpretations are possible. I plan to investigate these alternatives in a future paper on the Nebriini and related groups.

Dispersal potential.--N. chalceola and N. virescens adults have full-size hindwings and are probably capable of flight. N. pusilla members have highly reduced hindwings. Instances of flight and its significance for dispersal are at present unknown.

Natural history.--N. virescens life history is reviewed below. See Habu (1958) for data relating to life history of Palaearctic taxa.

Fossil record.--There is at present no fossil record for this lineage or any of its members.

3.4321 The virescens group

This group is represented by three extant species, named and discussed above. A single Nearctic species, N. virescens Horn, is described below.

3.43211 Nebria virescens Horn

(Figures 44-45, 54, 57, 61, 84, 155, 162, 182, 214, 225, 240, 249, 262, 290-291, 300, 305, 308, 315, 324, 345, 354, 381)

Nebria virescens Horn, 1870:100. HOLOTYPE, a female, in MCZ, labelled: "Van."/ "Type 652" [red label]/ "N. virescens Horn"/ "Holotype Nebria virescens Horn det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Vancouver, British Columbia.--Bänninger, 1925:261; 1949:153.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:47; 1924:21.--Csiki, 1927:368.--Hatch, 1939a:120; 1953:56.--Henshaw, 1885:4.--LeConte, 1878:476.--Leng, 1920:47.--Lindroth, 1961a:75; 1975:112.--Pratt and Hatch, 1938:192.--Schaupp, 1878:45.--Van Dyke, 1926:9.

Nebria virescens Chaudoir [an improper assignment of authorship].--Taylor, 1886:35.

Nebria brevis Casey, 1913:55. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "Corvallis, Oreg."/ "185"/ "Casey bequest 1925"/ "Lectotype brevis Csy. By C. H. Lindroth." TYPE LOCALITY.--Corvallis, Benton County, Oregon.--Bänninger, 1925:261.--Blackwelder and Blackwelder, 1948:2.--Casey, 1924:21.--Csiki, 1927:368.--Hatch, 1939a:120; 1953:56.--Leng, 1920:47.--Lindroth, 1961a:76; 1975:112.

Diagnostic combination.--Adults of this species can be distinguished from those of all other Nearctic taxa by the combination of character states given for recognition of virescens

lineage members. They can be distinguished from adults of other (i.e. Palaearctic) virescens group members by the following combination of character states: pronotal microsculpture isodiametric, moderately to deeply impressed; elytral microsculpture isodiametric, deeply impressed; penultimate labial palpomere bisetose; M3 setae of mentum present; length of metasternum greater than length of mesocoxal cavity; anterior metasternal process not margined medially; plane of lateral wing posterior to coxal ridge of hind coxa not completely vertical; males with two pairs of paramedial setae on sixth visible sternum; male genitalia: median lobe with mid-shaft (lateral aspect) thick; left paramere long and broad; female genitalia: eighth abdominal sternum apical margin with many long and medium length setae medially, basal apodeme deeply emarginate, lateral arm reduced to short lobe; paraprocts broadly fused with valvifers basally.

Description of form and structure.--Size small to medium, standardized body length males 7.5 to 10.1 mm, females 9.8 to 11.2 mm. Pronotum relatively large and wide, elytra moderately long and wide.

Color. Body uniformly brown or piceus, legs and head appendages slightly paler.

Reflection. Head, pronotum, and elytra moderately to markedly metallic blue or green; prothoracic venter faintly metallic in most members.

Luster. Head moderately dull or slightly shiny; pronotum and elytra dull.

Microsculpture. Dorsum with isodiametric meshes, faintly to moderately impressed on head, deeply impressed on pronotum and elytra.

Head. Frons smooth, frontal furrows linear shallow, broad; eyes moderately convex; antennae with basal four antennomeres without pubescence (except at apex of fourth antennomere in very few individuals), scape medium length, narrowed basally; anterior margin clypeus weakly, evenly concave; anterior margin labrum truncate or slightly bisinuate; penultimate labial palpomere bisetose; M3 setae present at basolateral angles of mentum; submentum with three pairs of lateral and one pair of medial setae across anterior margin.

Prothorax. Pronotum, shape semiovoid, convex; lateral margin markedly arcuate, basal sinuation absent or short and very shallow; lateral explanation broad throughout, slightly widened anteriorly; basal margin long, truncate (straight); apical angles medium length, broad, rounded; basal angles obtuse; anterior margination moderately impressed; lateral bead wide, shallowly impressed, obliterated basally; anterior transverse impression broad, shallow, smooth or faintly rugulose; median longitudinal impression moderately impressed; posterior transverse impression moderately deep, anteriorly deflected at middle; basal foveae broad with or without double etched lines separated by low convexity, carinate or not laterally; prosternum and proepisternum smooth, impunctate; prosternal intercoxal process margined basally only.

Pterothorax. Elytra slightly convex, with silhouette subrectangular; basal margination medium to long, straight to

moderately concave anteriorly; humeri moderately to markedly angulate; humeral carina absent or present as small denticle; subhumeral lateral sinuation shallow; subapical lateral sinuation shallow; apices narrowly rounded, medially straight, apposed in midline; medial striae shallowly or moderately impressed, lateral striae very faintly impressed, densely but minutely punctulate or weakly punctate; intervals flat or very slightly convex; hindwing full-sized; length of metasternum greater than length of mesocoxal cavity; anterior metasternal process not margined medially.

Legs. Plane of lateral wing posterior to coxal ridge of hind coxa not completely vertical; middle tibia deeply sulcate dorsally from base to near apex.

Abdomen. Males with two pairs of paramedial setae on sixth visible sternum; first visible sternum smooth, impunctate.

Male genitalia. Median lobe with mid-shaft (lateral aspect) thick; preapical-shaft (lateral aspect) moderately broad, moderately tapered apically, symmetrical (apical orifice directed dorsally) (apical and dorsal aspects); apex symmetrical, shovel-shaped, without marginal tooth (ventral aspect), short and sharply pointed (lateral aspect); parameres approximately symmetrical, equal in length (i.e. left paramere relatively long and broad, right paramere relatively short and broad).

Female genitalia. Eighth abdominal sternum apical margin with many long and medium length setae medially, basal apodeme width medium, deeply emarginate, lateral arm reduced to short lobe; proctiger hemispheric, membranous apically; paraprocts broadly fused

with valvifers basally; stylus broad, moderately arcuate, spatulate apically (ventral aspect), very broad, broadly rounded apically, straight (lateral aspect); setae in ventral diagonal row on coxite long and spiniform; setae in mediodorsal row on stylus long and spiniform, mediodorsal row diagonal; coxostylus densely setose at middle of medial surface only; bursa copulatrix with main axis slightly deflected dorsally, spermathecal chamber long, thick, with parallel sides (lateral aspect).

Sexual dimorphism.--As described for genus.

Geographical distribution.--Fig. 381 ; restricted to Pacific Coast region from southwestern British Columbia to California; south in California only at high altitude in the Sierra Nevada; range extends east across Columbia Plateau to western edge of Rocky Mountain region in westcentral Idaho (see Appendix B for list of localities).

Geographical variation.--Adults in populations in northeastern California (e.g. Modoc County) are, in general, larger and more vividly metallic blue (almost deep purple) than adults from most other areas. See also comments under ecophenotypic variation.

Geographical relations with allied taxa.--Although the geographical range of *N. virescens* is broadly sympatric with several other Nearctic *Nebria* taxa (see Table 5), closely related taxa are restricted to Japan, and their ranges are therefore allopatric.

Habitat distribution.--Macrohabitat range of this species is very broad--from Transition to Arctic/Alpine Zone. Members appear to be most abundant in Canadian Zone habitats however. Relationships,

if any, between individuals living in widely different life zones are at present unclear (see below). Microhabitat range of *N. virescens* is also impressively great. Adults have been collected in moist meadows, forest litter, stream banks, cracks on weathered sea cliffs, talus slopes, and at the edges of snowfields. In general, members of this species do not appear to require association with water bodies; but they do require cool, humid microhabitats.

Ecophenotypic variation.--Adults collected in high-altitude localities are, in every instance, smaller than average. For example, the specimen from Bunker Hill Lookout (Okanogan County, Washington), collected at 2120 m is the smallest known specimen; and the specimen I collected on Mount Baker (Washington) at 1500 m is almost as small. These specimens also differ in having relatively narrowed and shortened elytra (although hindwings in these specimens are full-sized), narrowed pronota in which a basal sinuation of the lateral margin is better developed than in most adults, and a better developed denticle at each humeral angle. Because so few specimens have been collected from high altitude localities (a total of only five, from localities in Washington and the Sierra Nevada of California), I am yet unable to evaluate the status of these specimens. I have found no differences among characters of male or female genitalia by which to distinguish the high and lower altitude forms. Further collecting and study of additional specimens is needed.

Taxonomic notes.--Future review of the worldwide *Nebria* fauna may indicate that recognition of *N. virescens* as representing a

distinct group is justified. This taxon is strongly differentiated from its sister group, demonstrating 41 apotypic character states not shared with N. chalceola and N. pusilla (and the latter share 25 apotypic states not also shared with N. virescens). At present, however, I place these three taxa in a single group to emphasize relationships not recognized before.

Phylogenetic relationships--According to my cladistic analysis, this species represents the sister group of N. chalceola and N. pusilla.

Dispersal potential.--N. virescens adults have large, strong, very heavily sclerotized wings; and I have no doubt that they can fly. Whether or not flight is important for dispersal among these beetles is unknown.

Natural history.--Adults of this species have been collected in every month of the year except January (see Table 13). Teneral adults appear in spring (April through June). Adults kept under laboratory conditions for over six months deposited eggs in November and December, a period which, I suggest, corresponds well to the normal oviposition period in the field. Larvae emerge in November through January and overwinter in some larval instar. Some unknown portion of the adult population must also overwinter.

Fossil record.--To date, no specimens referable to this species have been found as fossils.

3.433 The gyllenhali lineage

This lineage is represented by at least 15, and perhaps 19 or more, extant species. Five of these species are endemic to North America, three are common to Eurasia and North America, and the remainder are restricted to northern, central, and/or eastern Asia. My uncertainty about total number of included species stems from an insufficient knowledge of the Palaearctic fauna with which to evaluate the status of one or more taxa (see further comments in sections on included species groups). Included in this lineage are taxa previously assigned to Lindroth's (1961a) "pallipes" (in part), "gyllenhali," "hudsonica," and "ovipennis" (in part) groups, or to subgenus Boreonebria Jeannel (1937). Shilenkov's (1975a) concept of subgenus Boreonebria corresponds almost exactly to this lineage as here conceived.

Diagnostic combination.--Adult members of this lineage can be recognized by the following combination of character states: frontal red spot(s) absent (except in all N. paradisi members and in few members of other paradisi group taxa); paraglossae indistinct, completely fused with ligula; pronotum moderately to markedly cordate, midlateral pronotal setae present; hind coxa with one pair of setae at base (except two or more in some N. paradisi and N. gouleti members); ventroapical margin of fourth hind tarsomere projected, lobate laterally; second through fifth visible abdominal sterna without anterior paralateral setae; male genitalia: median lobe with basal bulb quadrate, broadly open basally, mid-shaft axis bent less than 135°, apex (ventral aspect) pointed; dorsobasal piece present as

thin collar on basal bulb; female genitalia: basal apodeme of eighth sternum deeply emarginate, lateral arm slightly to moderately shortened; proctiger hemispheric, heavily sclerotized throughout; medial area of valvifer weakly sclerotized or membranous; coxite with setae of ventral diagonal row setiform; stylus with setae of mediodorsal row setiform, mediodorsal row longitudinal; bursa copulatrix without sclerite in dorsal wall of spermathecal chamber.

3.4331 The paradisi group

This group is represented by at least three, and perhaps five, extant species, only one of which is a member of (and endemic to) the Nearctic fauna (Fig. 413). The remaining taxa are restricted to Hokkaido (Japan) or the Kuril Islands. Taxonomic status of each of the Palaearctic members of this group (namely, N. sakagutii Nakane, N. shibanaii Ueno, N. shiretokoana Nakane, and N. gibbulosa Motschulsky) is yet uncertain; but in section 4.1 on phylogeny, I treat each as a distinct species for comparative purposes. Lindroth (1961a) included N. paradisi in his "ovipennis" group. Erwin and Ball (1972) recognized the monophyly of that group exclusive of N. paradisi and, therefore, removed the latter (but left it unplaced). Shilenkov (1975a) considered only N. gibbulosa, and assigned it to subgenus Boreonebria.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: relative width pronotum medium or slightly broad; relative width elytra medium; mandibles moderately explanate basolaterally; mentum

with M2 setae moderately distant from basal margin; pronotum with apical angles moderately or very long, basal foveae slightly or moderately divergent basally; elytral silhouette ovoid, humeri markedly or extremely rounded, humeral carinae distinct, sharp, slightly to moderately projected, third, fifth, and seventh intervals uniform, uninterrupted (except faintly catenate in N. paradisi members); hindwing highly reduced, either very thin, elongate, strap-like or very short, scale-like; legs markedly long; male genitalia: median lobe with mid-shaft cylindrical, thickness approximately equal throughout, shape (in cross-section) circular, preapical-shaft (lateral aspect) moderately broad and tapered, apex (ventral aspect) broadly or bluntly pointed; female genitalia: spermathecal duct with distal portion narrow or moderately or extremely thickened, insertion of duct slightly right of midline (except in midline in N. paradisi females) on spermathecal chamber of bursa copulatrix.

3.43311 Nebria paradisi Darlington

(Figures 86, 145, 164, 252, 264, 303, 312, 340, 382)

Nebria columbiana; auctorum (not Casey).--Blackwelder and Blackwelder, 1948:2.--Hatch, 1939a:121; 1953:59.--Lindroth, 1961a:87.--Van Dyke, 1919:8 (in part); 1926:10 (in part).

Nebria kincaidi; auctorum (not Schwarz).--Bänninger, 1925:264; 1933:81; 1949:148.--Blackwelder, 1939:12.--Hatch, 1939a:121; 1953:59.--Lindroth, 1961a:87.--Ueno, 1955:47.

Nebria vandykei Darlington, 1930:104 [preoccupied by Nebria vandykei

Bänninger, 1928:5]. HOLOTYPE, a male, in MCZ, labelled: "Mt. Rainier, Was. VII 18, 27, Darlington"/ "Holotype ♂ Nebria vandykei Darlington" [red label]/ "P. J. Darlington Collection"/ "Nebria paradisi Darl.." Allotype also in MCZ. TYPE LOCALITY. --Paradise Valley (1830m), Mount Rainier National Park, Washington.--Bänninger, 1933:81.--Blackwelder, 1939:12.--Csiki, 1933:630.--Darlington, 1931a:24.--Döbler, 1975:146.--Hatch, 1939a:121; 1953:59.--Leng and Mutchler, 1933:11.--Lindroth, 1961a:87.--de Ruette, 1970:15.--Ueno, 1955:47.

Nebria paradisi Darlington, 1931a:24 [as a replacement name for N. vandykei Darlington].--Bänninger, 1933:81; 1949:148.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1933:630.--Erwin and Ball, 1972:81.--Hatch, 1939a:121; 1953:59.--Leng and Mutchler, 1933:11.--Lindroth, 1961a:87.--Mann, 1978:12.--de Ruette, 1970:15.--Ueno, 1955:47.

3.4332 The hudsonica group

This group is represented by three extant species, all endemic to North America (Fig. 415). One is restricted to eastern and the other two to western North America. Taxa included in this group were assigned by Lindroth (1961a) to his "hudsonica" and "pallipes" (in part) groups.

Disgnostic combination.--Adult members of this group can be recognized by the following combination of character states: pronotum and elytra markedly broad in relation to their respective lengths; mandibles broadly explanate basolaterally; mentum with M2

setae near basal margin; pronotum with apical angles moderately long, basal foveae parallel; elytral silhouette rectangular, humeri rectangular, humeral carinae absent or very vague and linear, third, fifth, and seventh intervals uniform, uninterrupted; hindwing full-sized; legs medium length; male genitalia: median lobe with mid-shaft moderately narrowed apically, shape (in cross-section) slightly compressed, preapical-shaft (lateral aspect) narrow, margins almost parallel, apex (ventral aspect) narrowly pointed; female genitalia: spermathecal duct with distal portion narrow, insertion of duct in midline on spermathecal chamber of bursa copulatrix.

3.43321 Nebria gouleti Kavanaugh, NEW SPECIES
(Figures 24, 171, 219, 238, 286, 292, 293, 302, 383)

Nebria gouleti, new species. HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Asotin Co., Hwy. 129, 10 mi. sw. Anatone, Rattlesnake Cr., 3000', 25 August 73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gouleti Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12504." Allotype (same data as holotype) also in CAS. 514 paratypes (see Appendix B for locality data) are deposited in the following collections: AMNH, ANSP, BFCa, CAS, CUIC, DHKa, DJLa, LRus, MCZ, MSU, OSUO, PURC, RTBe, SJSC, UASM, UIMI, UMMZ, USNM, UWBM, WSU. TYPE LOCALITY.--Rattlesnake Creek (10 miles southwest of Anatone), Asotin County, Washington.

Derivation of taxon name.--I take great pleasure in naming this

species in honor of my good friend and frequent field companion, Henri Goulet, from whom I have learned to observe and appreciate carabid beetles while they are alive!

3.43322 Nebria hudsonica LeConte

(Figures 10,25,49,51,62,65,169,170,199,255,256,325,346,384)

Nebria hudsonica LeConte, 1863b:3. LECTOTYPE (here designated), a male, in MCZ, labelled: "Saskatchewan"/ "Type 643" [red label]/ "N. hudsonica LeC."/ "Lectotype Nebria hudsonica LeConte designated by D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY. --Saskatchewan, Hudson's Bay Territory; here restricted to North Saskatchewan River (at Rocky Mountain House), Alberta.--Armin, 1963:91.--Bänninger, 1925:279; 1931:178.--Beaulne, 1914:30.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:360.--Edwards, 1975:49.--Erwin and Ball, 1972:78.--Fall, 1926:130.--Fall and Cockerell, 1907:156 (cannot refer to this species, but otherwise uninterpretable).--Gemminger and Harold, 1868:50.--Hatch, 1933:7; 1939a:117; 1953:55.--Henshaw, 1881:206; 1885:4.--Horn, 1870:102.--LeConte, 1863a:2; 1878:476.--Leng, 1920:47.--Lindroth, 1961a:83.--Putnam, 1876a:191.--Schaupp, 1878:45.--Van Dyke, 1925:122; 1926:10.--Wickham, 1893:228.

Notes on nomenclature and types.--In 1863, the area now occupied by the Province of Saskatchewan was part of Hudson's Bay Territory (or the Northwest Territories); and at least up to that date, the name "Saskatchewan" was apparently applied only to the Saskatchewan River system. Therefore, LeConte's use of the term probably refers to the

river system rather than the province. Only the Alberta stretches of the system are within the continuous range of _N. hudsonica_, although I have seen two specimens from the Province of Saskatchewan. My selection of North Saskatchewan River at Rocky Mountain House as the restricted type locality reflects these facts.

3.43323 _Nebria lacustris_ Casey

Nebria lacustris lacustris Casey

(Figures 12, 87, 165, 384)

Nebria pallipes; auctorum (not Say).--Casey, 1913:56.--LeConte, 1878:477 (as "race 2.").--Leonard, 1928:11 (in part).--Lindroth, 1961a:77.--Wickham, 1909:5.

Nebria lacustris Casey, 1913:56. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Bayfld, Wis, Wickham." / "Casey bequest 1925"/ "Type USNM 46865" [red label]/ "lacustris Csy."/ "Lectotype lacustris Csy. By C. H. Lindroth." TYPE LOCALITY.--Bayfield, Bayfield County, Wisconsin.--Bänninger, 1925:260;1949:147.--Bell, 1955:265 (in part).--Csiki, 1927:362.--Darlington, 1943:60.--Larochelle, 1975:94; 1977:112. --Leng, 1920:47.--Lindroth, 1961a:77; 1963a:76; 1969d:1109; 1975:112.--Spence, 1974:6.--Spence, Bell and Bell, 1976:81.--Spence and Bell, unpublished manuscript.

Nebria expansa Casey, 1913:56. LECTOTYPE (designated by Lindroth, 1975:112, and amended in an addendum to same paper p. 147), a female, in USNM, labelled: "L."/ "Casey bequest 1925"/ "expansa - 2 Paratype USNM 46864" [red label]/ "Lectotype expansa Csy.

By C. H. Lindroth." TYPE LOCALITY.--Indiana; here restricted to Turkey Run State Park, Parke County, Indiana.--Bell, 1955:265.--Csiki, 1927:357.--Larochelle, 1975:94.--Leng, 1920:47.--Lindroth, 1961a:77; 1969d:1109; 1975:112 and 147.--Spence, 1974:12.--Spence and Bell, unpublished manuscript.

Nebria sahlbergi; Leonard, 1928:211.

Nebria suturalis; Leonard (not LeConte), 1928:211.

Notes on nomenclature and types.--The name _N. lacustris_ has priority over _N. expansa_ by precedence of position as well as by action of the first reviser (Bell, 1955:265; see also Lindroth, 1961a:77).

In his original description, Casey recorded _expansa_ from "Texas and Indiana," based on his study of two females. Bell (1955:267) and Lindroth (1961a:77 and 1975:112) accepted the record from Texas. In my judgment, this record is erroneous. Acting on my suggestion, Lindroth (1975:147) amended his lectotype designation (1975:112) and selected the specimen labelled "L.", interpreted by Casey as from Indiana, instead of the "Texas" specimen. The _expansa_ form of _N. lacustris lacustris_ has frequently been collected at Turkey Run State Park, my choice as the restricted type locality.

Nebria lacustris bellorum Kavanaugh, NEW SUBSPECIES

(Figures 88, 309, 384)

Nebria lacustris; Bell, 1955:265 (in part).

Nebria lacustris bellorum, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Tenn., Great Smoky Mts. N. P., Chimneys Picnic

Area, W. Prong Little Pigeon R., 3000', 24May73 DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria lacustris bellorum Kavanaugh det. D. H. Kavanaugh 1976: [red label]/ "California Academy of Sciences Type No. 12506." Allotype (same data as holotype) also in CAS. 262 paratypes (see Appendix B for locality data) are deposited in the following collections: CAS, CUIC, DHKa, HoKn, MCZ, RTBe, TCBa, UAFA, UASM, USNM. TYPE LOCALITY.--West Prong Little Pigeon River (at Chimneys Picnic Area), Great Smoky Mountains National Park, Tennessee.

Derivation of taxon name.--I take pleasure in naming this subspecies in honor of Ross and Joyce Bell (Burlington, Vermont), who have long been interested in the systematics of eastern Nebria taxa, and who have generously provided encouragement and information for this study.

3.4333 The gyllenhali group

This group is represented by at least nine, and perhaps 11 or more, extant species. Only one of these species is endemic to North America, three are common to North America and Eurasia, and the remainder are endemic to northern, central, and/or eastern Asia (Fig. 416). The latter include N. subdilatata Motschulsky, N. baicalica Motschulsky, N. uralensis Glasunow, N. biseriata Lutshnik, and N. daisetsuzana Ueno. According to Shilenkov (1975a), N. rubrofemorata Shilenkov and N. sajanica Bänninger (both restricted to central Asia) should also be considered members of this group; but I have not yet

studied specimens representing these species. Except for the addition of the endemic Palaearctic species and a change in status of one taxon, this group is identical (at the species level) to Lindroth's (1961a) "gyllenhali" group.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: relative pronotal width medium to slightly broad (except extremely wide in N. subdilatata members); relative elytral width medium to moderately broad; mandibles moderately explanate basolaterally; mentum with M2 setae near basal margin; pronotum with apical angles medium in length, basal foveae parallel; elytral silhouette varied, rectangular to ovoid, shape of humeri varied, from rectangular to moderately rounded, humeral carinae absent, vague, or distinct but not projected, third, fifth, and/or seventh interval(s) faintly to moderately catenate; hindwing full-sized or variously reduced; legs medium length, slightly short, or slightly long; male genitalia: median lobe with mid-shaft moderately narrowed apically, shape (in cross-section) slightly compressed, preapical-shaft (lateral aspect) narrow or very narrow, margins almost parallel, apex (ventral aspect) broadly or bluntly pointed; female genitalia: spermathecal duct with distal portion slightly to greatly thickened, insertion of duct slightly or markedly right of midline or slightly left of midline on spermathecal chamber of bursa copulatrix.

3.43331 The _nivalis_ subgroup

3.433311 _Nebria nivalis_ (Paykull)

Nebria nivalis nivalis (Paykull)

(Figures 46-47, 89, 320, 344, 385-386)

Carabus nivalis Paykull, 1790:52. LECTOTYPE (here designated), a male, in NRSS, labelled: "Mus. Payk."/ "Riksmuseum Stockholm" [green label]/ "Lectotype Carabus nivalis Paykull designated by D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Lule Lappmark, Norrbotten Län, Sweden.--Paykull, 1798:119 (in part). --Schönherr, 1806:197.--Stephens, 1828:61.

Nebria nivalis (Paykull).--Andersen, 1970:89.--Bänninger, 1923:132; 1925:260; 1949:143.--Blair, 1950:220.--Csiki, 1927:364.--Gemminger and Harold, 1868:51.--Hågvar and Østbye, 1974:118.--Hamilton, 1889:93.--Henshaw, 1885:4.--Heyden, 1880-81:14.--Horn, 1870:104.--Horvatovitch, 1973:251.--Jeannel, 1937:4.--Larochelle, 1975:94 (in part); 1977:112 (in part).--Larsson and Gigja, 1959:15.--LeConte, 1863:2; 1878:476.--Leng, 1920:47.--Lindroth, 1939:54; 1961a:81 (in part); 1963a:28, 68 (in part); 1963b:125; 1969a:1109; 1974:30.--Matthews, 1977:302.--Motschulsky, 1846:125; 1850:72; 1865:275.--Poppius, 1905:17; 1910:302.--Sahlberg (J.), 1885:47.--Schaupp, 1878:46.--Shilenkov, 1974:50; 1975a:839; 1975b:61; 1976:117.--Van Dyke, 1940:256.

Nebria bifaria Mannerheim, 1853:120. LECTOTYPE (here designated), a male, in ZILR, labelled: "38"/ "Nebria carbonaria Esch. Insel.

Paul"/ "Lectotype ?" [red label]/ "Lectotype Nebria bifaria Mannerheim det. D. H. Kavanaugh 1977" [red label]. TYPE LOCALITY.--Saint Paul Island, Alaska.--Bänninger, 1923:132; 1925:260; 1949:144.--Beaulne, 1914:30.--Brown, 1937:107.--Casey, 1913:51.--Coope, 1970b:154.--Csiki, 1927:357.--Fall, 1926:130.--Gemminger and Harold, 1868:48.--Hamilton, 1889:93; 1894:7.--Hatch, 1939a:119.--Henshaw, 1885:4.--Heyden, 1880-81:13.--Horn, 1870:102.--Jeannel, 1937:5.--Larochelle, 1975:94.--LeConte, 1860:10; 1863:2; 1878:476.--Leng, 1920:46.--Lindroth, 1954c:366; 1961a:81 (in part).--Motschulsky, 1865:275.--Poppius, 1910:303.--Schaupp, 1878:45.--Shilenkov, 1975a:839; 1976:120.--Van Dyke, 1921:158; 1924:4; 1940:256.--Wickham, 1923:5.

Nebria carbonaria; auctorum (not Eschscholtz).--Beaulne, 1914:30.--Csiki, 1927:357.--Gemminger and Harold, 1868:48.--Hamilton, 1889:93; 1894:7.--Henshaw, 1885:4.--Heyden, 1880-81:13.--Larochelle, 1975:94.--LeConte, 1860:10.--Lindroth, 1961a:81.--Mannerheim, 1852:293; 1853:120.--Motschulsky, 1850:72 (in part); 1859:224.--Van Dyke, 1921:158.

Nebria femoralis Motschulsky, 1859:224 [preoccupied by Nebria femoralis Chaudoir, 1843:749]. LECTOTYPE (designated by Shilenkov, 1975a:389), in ZILR, not seen. TYPE LOCALITY.--Yakutsk, Yakutskaya A.S.S.R., U.S.S.R..--Bänninger, 1923:132; 1925:260.--Csiki, 1927:357.--Gemminger and Harold, 1868:49.--Heyden, 1880-81:13.--Jeannel, 1937:4.--Lindroth, 1955a:40; 1961a:82.--Motschulsky, 1865:275.--Poppius, 1910:303.--Shilenkov, 1975a:839; 1976:120.

Nebria femorata Motschulsky, 1865:275 [as a replacement name for N. femoralis Motschulsky].--Bänninger, 1923:132; 1925:260; 1949:144.--Csiki, 1927:358.--Gemminger and Harold, 1868:49.--Heyden, 1880-81:13.--Jeannel, 1937:4.--Larochelle, 1975:94.--Lindroth, 1955a:40; 1961a:82.--Sahlberg (J.), 1885:47.--Shilenkov, 1975a:839; 1976:120.

Nebria molbis Motschulsky, 1865:274 [an incorrect original spelling]. LECTOTYPE (here designated), sex undetermined [specimen incomplete, badly damaged], in ZMUM, labelled: "A. borealis" [green label]/ "Nebria mollis Motsch. Am. arct. cont." [green label]/ [red rectangle]. TYPE LOCALITY.--Alaska.--Csiki, 1927:389.--Lindroth, 1961a:82.

Nebria mollis Motschulsky [a justified emendation].--Csiki, 1927:389. --Gemminger and Harold, 1868:51.--Henshaw, 1885:4.--Horn, 1870:104.--Larochelle, 1975:94.--LeConte, 1878:473.--Leng, 1920:47.--Lindroth, 1961a:82.--Schaupp, 1978:46.--Shilenkov, 1976:120.

Nebria nivalis bifaria Mannerheim.--Lindroth, 1955a:39 (in part).

Notes on nomenclature and types.-- The specimen chosen as lectotype of Carabus nivalis is one of three specimens in NRSS from the Paykull Collection identified as nivalis. The other two specimens are actually individuals of N. gyllenhali gyllenhali (Schönherr). Because all three specimens bear identical labels and have been considered syntypes, the two gyllenhali gyllenhali specimens could perhaps be considered paralectotypes. Paykull (1798:119) subsequently described "variety β" of Carabus nivalis, which is clearly

synonymous with N. gyllenhali gyllenhali and was based on specimens from a different collector and locality. The original description of nivalis does not fit the two hetero-specific specimens, but the description of "variety β" does. I conclude that these specimens are probably not part of Paykull's original type series of nivalis; but they may be specimens he described as "variety β."

I have seen no published statement by Motschulsky indicating that his Nebria "molbis" was a misspelling. However, the type specimen is labelled "mollis"; and from as early as 1868, every subsequent citation of the name has been as "mollis." This suggests early recognition, possibly initiated (privately) by Motschulsky himself, of an original error. The first clear indication of an intended emendation is that of Csiki (1927:389).

Nebria nivalis gaspesiana Kavanaugh, NEW SUBSPECIES

(Figures 90, 251, 385-386)

Nebria suturalis; Leng (not LeConte).--Leng, 1920:47 (in part).--Lindroth, 1955a:39.

Nebria nivalis bifaria Mannerheim.--Lindroth, 1955a:39 (in part).

Nebria nivalis; auctorum.--Larochelle, 1972:62 (in part); 1976:48; 1977:12 (in part).--Lindroth, 1961a:81 (in part); 1971:1459.

Nebria bifaria; Lindroth, 1961:81 (in part).

Nebria nivalis gaspesiana, new subspecies. HOLOTYPE, a male, in CAS, labelled: "Can., Que., Peninsule de Gaspe, Mt. Albert, Ruisseau du Diable, 3200'-3500', 11-12 June 73 DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria

nivalis gaspesiana Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12510." Allotype (same data as holotype) also in CAS. 287 paratypes (see Appendix B for locality data) are deposited in the following collections: ALar, CAS, CNC, DBUM, DHKa, MCZ, RTBe, UASM, USNM. TYPE LOCALITY.--Ruisseau du Diable (980m-1070m), Mont Albert, Parc de La Gaspésie, Comté de Gaspé-Ouest, Québec.

Derivation of taxon name.--This subspecies is named for the Gaspé Peninsula, on which the type locality is found.

3.43332 The *gyllenhali* subgroup

3.433321 *Nebria crassicornis* Van Dyke

Nebria crassicornis crassicornis Van Dyke

(Figures 13, 92, 217, 326, 387)

Nebria crassicornis Van Dyke, 1925:121. HOLOTYPE, a male, in CAS, labelled: "Paradise Park Alt. 6000 ft."/ "Mt. Rainier Wash. VII, 14-31, 05"/ "Coll. by Van Dyke"/ "Van Dyke Collection"/ "Type Nebria crassicornis Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1627." Allotype (same data as holotype) also in CAS (California Academy of Sciences Type No. 1628). TYPE LOCALITY.--Paradise Park, Mount Rainier National Park, Washington.--Bänninger, 1928:6; 1931:178.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:388; 1933:631.--Hatch, 1939a:119; 1953:56.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:80.--Mann, 1978:20.--Van Dyke, 1926:10.

Nebria crassicornis intermedia Van Dyke, NEW STATUS

(Figures 14, 93, 352, 387)

Nebria labradorica; auctorum (not Casey).--Bänninger, 1928:6 (in part); 1931:178 (in part).--Hatch, 1939a:119 (in part); 1953:56. --Van Dyke, 1925:122 (in part); 1926:10 (in part).

Nebria intermedia Van Dyke, 1949:49. HOLOTYPE, a male, in CAS, labelled: "Logan Pass Glac. Nat. Pk VII-*-1938"/ "Van Dyke Collection"/ "Holotype No. 6008 Nebria intermedia Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 6008." Allotype (same data as holotype) also in CAS (CAS Type No. 6009). TYPE LOCALITY.--Logan Pass, Glacier National Park, Montana. NEW STATUS.--Edwards, 1975:49.--Hatch, 1953:56.--Lindroth, 1961a:80.

3.433322 Nebria gyllenhali (Schönherr)

Nebria gyllenhali gyllenhali (Schönherr)

Carabus gyllenhali Schönherr, 1806:196. LECTOTYPE (here designated), a male, in NRSS, labelled: "♂"/ [triangular blue label]/ "Lectotype Carabus gyllenhali Schönherr designated by D. H. Kavanaugh 1976" [red label]. Five paralectotypes (same data as lectotype) also in NRSS. TYPE LOCALITY.--Lake Vänern, Sweden.

Nebria gyllenhali (Schönherr).--Csiki, 1927:358.--Lindroth, 1939:59; 1955a:41; 1961a:78.

Notes on nomenclature and types.--N. gyllenhali gyllenhali is

restricted to the Palearctic Region. The literature on this subspecies is extensive and numerous synonyms have been recognized (see Jeannel, 1937:4; Lindroth, 1939:54). I have omitted a listing of synonymy and most references in this treatment both because they are inappropriate here and because there is still some question on the status of several of the proposed synonyms.

One nomenclatural problem must be considered, however, because it affects the validity of the species epithet and thereby the names of the three Nearctic subspecies. The name Carabus rufescens Ström (1768:331)did not appear in the literature between the date of its original description and 1880, when Schøyen (1880:183) revived its use. Jeannel (1937:4) accepted N. rufescens (Ström) as the senior synonym of Nebria gyllenhali (Schönherr); and following him, a number of authors have subsequently applied the name rufescens to this species (Blair, 1950:220; Friden, 1971:30; Greenslade, 1968:41; Horvatovitch, 1973:252; Luff, 1972:174; Luff and Davies, 1972:47; Nakane, 1963:18 and 1971:180; Ueno, 1953:59 and 1955:47). The combination N. rufescens gyllenhali has sporadically appeared (Jeanne, 1966:12; Jeannel, 1937:4 and 1941:19) as has the unfortunate combination N. gyllenhali rufescens, where rufescens referred variously to a subspecies, race, variety, or aberration of gyllenhali (Andrewes, 1939:161; Bänninger, 1925:345 and 1960:261; Csiki, 1927:359; Munster, 1933:267; Reitter, 1908:93).

Lindroth (1939:59, 1954b:121, and 1961:78) and Bänninger (1949:144) have refused to recognize N. rufescens as the valid name for this species. For the reasons they have cited, because no type

specimen has been found or perhaps ever existed, and because Ström's original description "cannot be interpreted (not even as a _Nebria_)" (Lindroth, personal communication), I agree that the name _gyllenhali_ (Schönherr) should be conserved as the valid name for the species. Any future use of the epithet _rufescens_ should be discouraged; and the name _Carabus_ _rufescens_ Ström should be listed as a _nomen_ _dubium_.

Nebria _gyllenhali_ _castanipes_ (Kirby)

(Figures 14A, 26, 93A, 191, 289, 319, 356, 388)

Helobia _castanipes_ Kirby, 1837:20. LECTOTYPE (here designated), a female, in BMNH, labelled: "Type" [red-trimmed disc]/ "70"/ "N. Amer. " [pale blue disc with "5699" on underside]/ "apparently Type of castanipes Kby. Lindroth 1952"/ "Lectotype Helobia castanipes Kirby designated by D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Nipigon, Lake Superior, Thunder Bay District, Ontario (designated by Lindroth, 1961a:78).--Horn, 1876:128.--Lindroth, 1953a:169.

Nebria _castanipes_ (Kirby).--Bänninger, 1925:279.--Csiki, 1927:367.--Hamilton, 1894:7.--Henshaw, 1881:206.--Horn, 1870:102.--Larochelle, 1975:94.--LeConte, 1848:447; 1850:209; 1863a:2; 1873:322.--Leng, 1920:46.--Lindroth, 1961a:78.--Melsheimer, 1853:11.--Provancher, 1877:148.--Schaupp, 1878:46.

Nebria _moesta_ LeConte, 1850:209. LECTOTYPE (here designated), a male, in MCZ, labelled: [light green disc]/ "Type 645" [red label]/ "N. moesta LeC."/ "N. castanipes Kby."/ "Lectotype Nebria moesta LeConte designated by D. H. Kavanaugh 1976" [red

label]. One male and two female paralectotypes (same data as lectotype) also in MCZ. TYPE LOCALITY.--Lake Superior, Ontario. --Bänninger, 1925:279.--Casey, 1913:51.--Csiki, 1927:367.--Darlington, 1943:60.--Fall, 1926:130.--Gemminger and Harold, 1868:51.--Hamilton, 1894:7.--Hatch, 1939a:120; 1953:58.--Henshaw, 1881:206.--Horn, 1870:102.--Larochelle, 1975:94.--LeConte, 1863a:2; 1863b:3; 1869:370; 1873:322.--Leng, 1920:46.--Leng and Mutchler, 1933:10.--Lindroth, 1939:61; 1953a:169; 1954b:121; 1954c:366; 1955a:40; 1961a:78; 1963a:28.--Mank, 1934:74.--Melsheimer, 1853:11.--Motschulsky, 1865:274.--Provancher, 1877:148.--Schaupp, 1878:46.

Nebria _sahlbergii_; _auctorum_ (not Fischer von Waldheim).--LeConte, 1853:400; 1878:479 (in part).--Packard, 1872:92; 1888:144.

Nebria _sahlbergi_; _auctorum_.--Beaulne, 1914:30 (in part).--Blackwelder and Blackwelder, 1948:2.--Blatchley, 1910:52.--Bowditch, 1896:2.--Casey, 1913:51; 1920:149.--Criddle, 1922:61. --Csiki, 1927:367 (in part).--Fall and Cockerell, 1907:156.--Hamilton, 1894:7 (in part).--Harrington, 1890:139, 190.--Hatch, 1939a:120 (in part).--Henshaw, 1881:206 (in part); 1885:4 (in part).--Horn, 1870:102; 1876:128 (in part); 1885:4 (in part).--Leng, 1920:46 (in part).--Leonard, 1928:211 (in part.--Lindroth, 1954c:366 (in part); 1955a:40; 1961a:78 (in part).--Poppius, 1910:303 (in part).--Schaupp, 1878:45 (in part).--Scudder, 1879:178B; 1890:532: 1895a:54.--Sherman, 1910:177(in

part).--Wickham, 1893:298.

Nebria gyllenhalii Motschulsky, 1865:274 [a misspelling].

Nebria elias Motschulsky, 1865:275. NOMEN DUBIUM. Type specimen destroyed (See discussion below); only labels survive: "Am. bor. occ. cont." [green label]/ "Nebria elias Motsch. Am. b. occ." [green label]/ [red rectangle]/ "Type specimen lost. Consider: Nomen Dubium designated by D. H. Kavanaugh 1977" [red label]. TYPE LOCALITY.--Alaska.--Bänninger, 1925:279.--Csiki, 1927:388.--Gemminger and Harold, 1868:49.--Henshaw, 1885:4.--Horn, 1870:104.--LeConte, 1878:473.--Leng, 1920:47.--Lindroth, 1961a:78.--Schaupp, 1878:46.

Nebria stahlbergi Knobel, 1895:9 [a misspelling].

Nebria labradorica Casey, 1920:151. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "W. St. Modest Labr."/ "Casey bequest 1925"/ "Type USNM 46855" [red label]/ "labradorica Csy." "Lectotype labradorica Csy. By C. H. Lindroth." TYPE LOCALITY.--West Saint Modest, Labrador, Newfoundland.--Bänninger, 1925:261; 1928:6 (in part).--Blackwelder and Blackwelder, 1948:2.--Brown, 1930:232.--Casey, 1924:20.--Csiki, 1927:360.--Hatch, 1939a:119 (in part); 1953:55.--Jeannel, 1937:5.--Larochelle, 1975:94.--Leng and Mutchler, 1927:8.--Lindroth, 1939:61; 1953a:169; 1954b:122; 1954c:366; 1955a:40; 1961a:78; 1975:112.--Van Dyke, 1924:5; 1925:122 (in part); 1926:10 (in part); 1949:49.

Nebria prominens Casey, 1920:151. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "N.H. Mt. W."/ "195/

"Casey bequest 1925"/ "Type USNM 46867" [red label]/ "prominens Csy."/ "Lectotype prominens Csy. By C. H. Lindroth." TYPE LOCALITY.--Mount Washington, Coos County, New Hampshire.--Csiki, 1927:389.--Larochelle, 1975:94.--Leng and Mutchler, 1927:8.--Lindroth, 1954b:122; 1954c:366; 1955a:40; 1961a:78; 1975:112.

Nebria curtulata Casey, 1924:20. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "W. St. Modest Labr."/ "♂"/ "Casey bequest 1925"/ "Type USNM 46856" [red label]/ "curtulata Csy."/ "Lectotype curtulata Csy. By C. H. Lindroth." TYPE LOCALITY.--West Saint Modest, Labrador, Newfoundland.--Csiki, 1927:360.--Larochelle, 1975:94.--Leng and Mutchler, 1927:8.--Lindroth, 1954b:122; 1954c:366; 1961a:78; 1975:112.

Nebria gyllenhali; auctorum.--Bänninger, 1928:6 (in part).--Edwards, 1975:49.--Kirk and Balsbaugh, 1975:15.--Larochelle, 1972:62; 1975:94; 1976a:48; 1976b:130; 1977:112.--Lindroth, 1961a:78; 1963a:28; 1969d:1109; 1975:112.

Nebria gyllenhali labradorica Casey.--Bänninger, 1931:128 (in part).

Nebria rufescens gyllenhali Schönherr.--Jeannel, 1937:4 (in part).

Nebria curtulana Jeannel, 1937:5 [a misspelling].

Nebria sahlbergi moesta LeConte.--Hatch, 1939a:120.--Lindroth, 1955a:40.

Nebria gyllenhali castanipes (Kirby).--Larsson and Gigja, 1959:14.--Lindroth, 1954c:366; 1955a:40.

Notes on nomenclature and types.--The lectotype of Helobia castanipes bears no labels in Kirby's hand. However, according to P. M. Hammond (personal communication), the number "5699" on the

underside of one label refers to an entry in manuscript catalogs of the Coleoptera in BMNH. An original label in Kirby's hand is pasted in the catalog at this entry and reads: "73. 1. ♀?/ castanipes." The fate of the second of the two specimens mentioned by Kirby in his original description is unknown.

The type specimen of N. elias has been completely destroyed and only its pin and labels remain (in ZMUM). Motschulsky's original description is too vague to permit certainty that N. elias and N. gyllenhali castanipes are synonymous. The occurrence of the latter in Alaska (the type area of N. elias) is relatively rare and local, which casts further uncertainty on the identity of N. elias. I therefore refrain from designation of a neotype and list N. elias as as a nomen dubium, but tentatively as a synonym of N. gyllenhali castanipes, following Lindroth (1961a:78).

Nebria gyllenhali lindrothi Kavanaugh, NEW SUBSPECIES

(Figures 28, 93B, 192, 356, 388)

Nebria sahlbergi; Wickham, 1902:232.

Nebria gyllenhali; auctorum.--Armin, 1963:90.

Nebria gyllenhali lindrothi, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Wyo., Albany Co., Medicine Bow Mts., Snowy Range, Brooklyn Lk., 10500', 11July 72 DHKavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gyllenhali lindrothi Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12512." Allotype (same data as holotype) also in CAS. 1387 paratypes

(see Appendix B for locality data) are deposited in the following collections: AMNH, ANSP, CArm, CAS, CNC, CUB, CUIC, DHKa, DRWh, EAMa, FMNH, ICCM, KSUC, KUSM, MCZ, MSU, PADA, PMCh, PMNH, PURC, RCGr, RDav, RTBe, SDSU, UAFA, UASM, USNM, UWBM, UWL, ZMLS. TYPE LOCALITY.--Brooklyn Lake (3200m), Albany County, Wyoming.

Notes on nomenclature and types.--This subspecies is the form noted by Lindroth (1969d:1109) as an undescribed species related to N. gyllenhali.

Derivation of taxon name.--I take great pleasure in naming this subspecies in honor of Carl H. Lindroth, a friend whose knowledge of and studies on Holarctic Carabidae have been a guiding light in this study, and who first called my attention to the distinctiveness of members of this taxon.

Nebria gyllenhali lassenensis Kavanaugh, NEW SUBSPECIES

(Figures 27, 388)

Nebria gyllenhali lassenensis, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., Lassen Volcanic N. P., Cascade Range, s. slope Mt. Lassen, Emerald Lk., 2450m, 22Aug.74 D.H. Kavanaugh Coll."/ "Holotype Nebria gyllenhali lassenensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12511." Allotype (same data as holotype) also in CAS. 34 paratypes (see Appendix B for locality data) are deposited in the following collections: CAS, DHKa, FMNH, USNM. TYPE LOCALITY.--Emerald Lake, Mount Lassen

(south slope), Lassen Volcanic National Park, California.

Derivation of taxon name.--This subspecies is named for Mount Lassen, on the south slope of which the type locality is found.

3.433323 Nebria frigida R. F. Sahlberg

(Figures 156, 197, 253-254, 327, 347, 389)

Nebria frigida R. F. Sahlberg, 1844:11. LECTOTYPE (designated by Lindroth, 1961:81), a female, in UMTF, labelled: "♀"/ [violet disc]/ "Ochotsk"/ "Coll. Sahlb."/ "Lectotypus frigida F. R. Sahlb. design. Lindroth" [red label]. TYPE LOCALITY.--Ochotsk (Marekan ["in monte Morikan"]), Khabarovskiy Kray, U.S.S.R..--Bänninger, 1923:133; 1925:261; 1949:;153.--Beaulne, 1914:30.--Csiki, 1927:358.--Gemminger and Harold, 1868:49.--Hamilton, 1894:7. Henshaw, 1887:1; 1895:1.--Heyden, 1880-81:14; 1893:12. --Leng, 1920:47.--Lindroth, 1961a:81; 1961b:442; 1963b:125; 1969a:1109; 1975:112.--Motschulsky, 1850:73; 1859:224.--Poppius, 1910:303.--Sahlberg (J.), 1885:47.--Shilenkov, 1975a:839.

Nebria viridis Horn, 1870:101. LECTOTYPE (here designated), a male, in MCZ, labelled: "R. [superscript "M"] A."/ "Type No. 1027-" [red label]/ "N. viridis Horn"/ "Lectotype Nebria viridis Horn designated by D. H. Kavanaugh 1976" [red label]. One male paralectotype (same data as lectotype) also in MCZ. TYPE LOCALITY.--Saint Michael, Alaska.--Bänninger, 1928:6; 1949:147.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:368.--Fall, 1926:130.--Hamilton, 1894:7.--Hatch, 1939a:119; 1939b:45; 1953:55.--Henshaw,--1885:4.--LeConte, 1878:476.--Leng,

1920:46.--Lindroth, 1961a:81; 1961b:442.--Poppius, 1910:303.--Schaupp, 1878:45.--Van Dyke, 1921:158; 1924:4.

Nebria parvula J. Sahlberg, 1885 (1887, according to Lindroth, 1969d:1109):47. LECTOTYPE (designated by Lindroth, 1961a:81), a female, in NRSS, labelled: "Porte Clarence"/ "Exped. Vega."/ "Spec. typ."/ "192" [yellow label]/ "Typus" [red label]/ "Nebria parvula J. Sahlb."/ "N. frigida F. Sbg. v. obscurata Popp. teste Poppius"/ "89 59" [red label]/ "Lectotypus parvula J. Sahlb. design. Lindroth" [red label]/ "Riksmuseum Stockholm" [green label]. TYPE LOCALITY.--Port Clarence, Alaska.--Bänninger, 1923:133; 1925:261.--Beaulne, 1914:30.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:51.--Csiki, 1927:358.--Hamilton, 1894:7.--Hatch, 1939a:119.--Henshaw, 1887:1; 1895:1.--Heyden, 1893:13; 1896:7.--Leng, 1920:46.--Lindroth, 1961a:81; 1969d:1109.--Poppius, 1910:303.--Van Dyke, 1924:5.

Nebria reducta Casey, 1920:150. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "˚A1"/ "Casey bequest 1925"/ "Type USNM 46866" [red label;/ "reducta Csy."/ "Lectotype reducta Csy. By C. H. Lindroth." TYPE LOCALITY.--Saint Paul Island, Pribilov Islands, Alaska.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:389.--Hatch, 1939a:119.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:81; 1975:112.--Van Dyke, 1921:158; 1924:5.

Notes on nomenclature and types.--In Horn's original description of N. viridis, only two specimens are mentioned. In MCZ, there are now three specimens (one from the Horn Collection, two from the

LeConte Collection). I have designated the Horn specimen as lectotype and the first LeConte specimen as the paralectotype. The second LeConte specimen (labelled "viridis 2") has no type status. All three specimens bear identical first labels; but LeConte may have received his second specimen directly from Ulke (see Horn, 1870:14), his first specimen from Horn.

I see no reason to doubt the record of N. frigida from St. Paul Island (type locality of N. reducta), although Lindroth's (1961a:21, 81 and 1975:112) comments on the general reliability of some older records from that area must be considered.

3.434 The gregaria lineage

This lineage is represented by 23 extant species, five of which (N. carbonaria Eschscholtz, N. snowi Bates, N. angustula Motschulsky, N. altaica Gebler., and N. ochotica Sahlberg) are restricted to eastern and/or central Asia. [I am not yet convinced that N. ochotica and N. japonica Bates are conspecific, and I therefore treat these as separate species in section 4.1 on phylogeny.] Included in this lineage are taxa previously assigned to Lindroth's (1961a) "gregaria," "obtusa," "mannerheimi," "pallipes," (in part) and "appalachia" groups or to subgenus Reductonebria Shilenkov (1975a).

Diagnostic combination.--Adult members of this lineage can be recognized by the following combination of character states: frontal red spot(s) present; paraglossae indistinct, completely fused with ligula; pronotum moderately to faintly cordate, midlateral pronotal setae absent; hind coxa with two or more pairs of setae at base;

ventroapical margin of fourth hind tarsomere projected, lobate; second through fifth visible abdominal sterna without anterior paralateral setae; male genitalia: median lobe with basal bulb quadrate, broadly open basally, mid-shaft axis bent less than 135°, apex (ventral aspect) pointed; dorsobasal piece present as thin collar on basal bulb; female genitalia: basal apodeme of eighth sternum deeply emarginate, lateral arm not or moderately shortened; proctiger hemispheric, heavily sclerotized throughout; medial area of valvifer weakly sclerotized; coxite with setae of ventral diagonal row setiform; stylus with setae of mediodorsal row setiform, mediodorsal row longitudinal; bursa copulatrix with sclerite, varied in size and shape, in dorsal wall of spermathecal chamber.

3.4341 The *gregaria* group

This group is represented by 11 extant species, three of which (*N. carbonaria*, *N. snowi*, and *N. angustula*) are restricted to extreme eastern Asia (specifically, to Kamchatka and/or the northern Kuril Islands). The remaining species are restricted to western North America (Fig. 414). Except for the addition of the Palaearctic species, this group is identical (at the species level) in composition to Lindroth's (1961a) "*gregaria*" group.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: head faintly shiny; pronotum with basal sinuation of lateral margin moderately long, width of lateral explanation medium (except narrow in *N. lyelli* members); male genitalia: median lobe with mid-shaft

cylindrical or slightly narrowed basally, shape (in cross-section) slightly compressed (except markedly compressed in _N. angustula_ males), ventral margin of preapical-shaft (lateral aspect) straight or evenly concave, or abruptly deflected ventrally near apex, apex (ventral aspect) broadly pointed (except narrowly pointed in _N. snowi_, _N. carbonaria_, and _N. lyelli_ males); female genitalia: bursa copulatrix with spermathecal chamber (dorsal aspect) spatulate or broadly cordate, insertion of spermathecal duct posterior/ventral.

3.43411 The _lyelli_ subgroup

3.434111 _Nebria lyelli_ Van Dyke

(Figures 29, 66, 94, 189, 310, 390)

Nebria lyelli Van Dyke, 1925:120. HOLOTYPE, a male, in CAS, labelled: "Mt. Lyell, Yosemite Pk. Cal. VII-13-1921"/ "Van Dyke Collection"/ "Type Nebria lyelli Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1626." TYPE LOCALITY.--Mount Lyell (3350m), Yosemite National Park, California.--Blackwelder, 1939:12.--Csiki, 1927:388; 1933:631.--Darlington, 1930:105.--Kavanaugh, 1971:44.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:72.--Van Dyke, 1926:11.

3.434112 _Nebria acuta_ Lindroth

Nebria acuta acuta Lindroth

(Figures 95, 157, 265, 328, 390)

Nebria acuta Lindroth, 1961a:71. HOLOTYPE, a male, in MCZ, labelled:

"Alaska. 16 mi. E. Valdez. 439 20.VIII.1958 Lindroth"/ "M.C.Z. Type 30428" [red label]/ "Holotypus acuta Lth." [red label]. TYPE LOCALITY.--Snowslide Gulch (16 miles east of Valdez), Alaska.--de Ruette, 1970:15.

Nebria acuta quileute Kavanaugh, NEW SUBSPECIES
(Figures 95, 266, 329, 390)

Nebria acuta Lindroth, 1961a:71 (in part).

Nebria acuta quileute, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Olympic N. P., Olympic Mts., Boulder Cr. at Olympic Hot Springs, 2000', 20July71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria acuta quileute Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12494." Allotype (same data as holotype) also in CAS. 132 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, CNC, DHKa, LACM, MCZ, UASM, UIMI, USNM, UWBM. TYPE LOCALITY.--Boulder Creek (at Olympic Hot Springs), Olympic National Park, Washington.

Derivation of taxon name.--This subspecies is named for the people native to the area including the type locality, the Quileute tribe.

3.43412 The _sahlbergii_ subgroup

3.434121 _Nebria sahlbergii_ Fischer von Waldheim

Nebria sahlbergii sahlbergii Fischer von Waldheim

(Figures 158, 267, 329A, 391)

Nebria sahlbergii Fischer von Waldheim, 1828:254. LECTOTYPE (here designated), a male, in UMHF, labelled: "♂"/ "Eschsch."/ "Sitka"/ "Lectotype Nebria sahlbergii Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]/ "Lectotype Nebria violacea Motsch. designated by D. H. Kavanaugh 1977" [red label]. TYPE LOCALITY.--Sitka, Baranof Island, Alaska.--LeConte, 1960:10; 1878:479 (in part).--Melsheimer, 1853:11.--Motschulsky, 1850:72.

Nebria sahlbergii Eschscholtz [an improper assignment of authorship]. --Dejean, 1831:576.--Fischer von Waldheim, 1828:254.--Mannerheim, 1843:189.--Motschulsky, 1865:274.

Nebria sahlbergi Eschscholtz [unjustified emendation and an improper assignment of authorship].--Menetries, 1844:54.

Nebria violacea Motschulsky, 1850:73. LECTOTYPE (here designated), a male, in UMHF, labelled: "♂"/ "Eschsch."/ "Sitka"/ "Lectotype Nebria sahlbergii Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]/ "Lectotype Nebria violacea Motsch. designated by D. H. Kavanaugh 1977 [red label]. TYPE LOCALITY.--Sitka, Baranof Island, Alaska.--Csiki, 1927:367.--Gemminger and Harold, 1868:52.--Leng, 1920:46.--Lindroth, 1961a:68.

Nebria sahlbergi; auctorum [unjustified emendation].--Bänninger,

1925:259; 1949:147.--Beaulne, 1914:30 (in part).--Blackwelder and Blackwelder, 1948:2 (in part).--Clark, 1948:25.--Csiki, 1927:367 (in part).--Eschscholtz, 1833:23.--Fall, 1926:129.--Gemminger and Harold, 1868:52.--Hamilton, 1894:7 (in part).--Hardy, 1927:C22.--Hatch, 1939a:120 (in part); 1953:58.--Henshaw, 1881:206 (in part); 1885:4 (in part).--Horn, 1870:102 (in part); 1876:128 (in part).--Jeannel, 1937:4.--LeConte, 1878:476.--Leng, 1920:46 (in part).--Lindroth, 1954b:121; 1961a:68; 1963b:123.--Poppius, 1910:303 (in part).--Schaupp, 1878:45 (in part).--Sherman, 1910:177 (in part).--Van Dyke, 1919:8; 1924:5; 1925:120; 1926:9.--Venables, 1913:268.

Nebria gregaria; Schwarz, 1900:524 (in part).

Nebria aleuta Van Dyke, 1924:5. HOLOTYPE, a male, in CAS, labelled: "Mt. Makushin, Unalaska I. Alaska VII-3-1907"/ "E. C. Van Dyke Collector"/ "Van Dyke Collection"/ "Type Nebria aleuta Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 3342." TYPE LOCALITY.--Mount Makushin, Unalaska Island, Aleutian Islands, Alaska.--Blackwelder and Blackwelder, 1948:2. --Hatch, 1939a:120.--Leng and Mutchler, 1933:11.--Lindroth, 1961a:68.

Nebria violaceus Fall, 1926:129 [a misspelling].

Notes on nomenclature and types.--Fischer's description of N. sahlbergii was based on study of Eschscholtz's material (Fischer, 1828:254). I have found only two specimens probably representing the original type series--one in the Fischer collection (ZMUM), the other in the Mannerheim collection (UMHF). I have chosen the UMHF specimen

as lectotype because, first, the original description better fits this specimen, and second, the Fischer specimen is, in fact, a representative of N. gyllenhali (Schönherr) rather than N. sahlbergii as the latter name has been applied (Lindroth, 1961a). The Fischer specimen must be considered a paralectotype of N. sahlbergii in spite of its identity. In fact, the strange misuse of the name N. sahlbergii by numerous North American authors in referring to N. gyllenhali castanipes (Kirby) (see synonymy under this latter name) can only now be explained--that is, if these authors considered the Fischer specimen as the type for N. sahlbergii.

An additional result of the mixed nature of Fischer's type series is as follows. Mannerheim obtained one of Eschscholtz's specimens, probably studied the other specimen in Fischer's collection, and then noted (1843:189) that two 'varieties' existed. He called the form represented by the Eschscholtz specimen in his possession "var. B." Motschulsky (1850:73), referring to Mannerheim's brief description of variety "B," named this form N. violacea. Consequently, the specimen now in UMHF appears to be the specimen upon which both N. violacea and N. sahlbergii are based! I have, therefore, designated (and so labelled) the specimen as lectotype for both names.

Nebria sahlbergii modoc Kavanaugh, NEW SUBSPECIES

(Figures 97, 124, 203, 330, 391)

Nebria sahlbergii modoc, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Calif., Modoc Co., Warner Mts., 4 mi. e. New Pine Creek, Pine Cr., 5700', 22May71 DHKavanaugh & EAMartinko"/

"D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria sahlbergii modoc Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12513." Allotype (same data as holotype) also in CAS. 11 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, UASM, USNM. TYPE LOCALITY.--Pine Creek (4 mmles east of New Pine Creek), Modoc County, California.

Derivation of taxon name.--This subspecies is named for the county which includes the type locality, as well as for the people native to the region.

Nebria sahlbergii triad Kavanaugh, NEW SUBSPECIES

(Figures 98, 391)

Nebria sahlbergii triad, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., Trinity Co., Trinity Alps, S. F. Salmon R. at Big Flat Cmpgd., 1490m, 18July75 D.H. & B.A. Kavanaugh Stop #75-36"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria sahlbergii triad Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12514." Allotype (same data as holotype) also in CAS. 212 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, FMNH, MCZ, PUCA, UASM, USNM. TYPE LOCALITY.--South Fork Salmon River (at Big Flat Campground), Trinity County, California.

Derivation of taxon name.--This subspecies is named for the Trinity Alps, in which the type locality is found. I use a synonym

of 'trinity' for this purpose.

3.43413 The <u>gregaria</u> subgroup

3.434131 <u>Nebria</u> <u>gregaria</u> Fischer von Waldheim

(Figures 11, 15, 53, 67, 129, 141, 186, 311, 393)

<u>Nebria</u> <u>gregaria</u> Fischer von Waldheim, 1821:72. LECTOTYPE (here designated), a male, in ZMUM, labelled: "47. gregaria Fisch."/ "Lectotype Nebria gregaria Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]. TYPE LOCALITY.--Unalaska, Unalaska Island, Aleutian Islands, Alaska.--Bänninger, 1925:259; 1928:2; 1949:147.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:47.--Csiki, 1927:358.--Dejean, 1931:575.--Eschscholtz, 1823:101.--Gemminger and Harold, 1868:49.--Hamilton, 1894:6.--Hatch, 1938:145; 1939a:120.--Henshaw, 1885:4.--Horn, 1870:100.--Jeannel, 1937:4.--LeConte, 1860:10.--Leng, 1920:46.--Lindroth, 1961a:66; 1963b:123; 1975:111.--Melsheimer, 1853:11.--Schaupp, 1878:45.--Van Dyke, 1925:121.

<u>Nebria</u> <u>gregaria</u> Eschscholtz [an improper assignment of authorship].--Dejean, 1826:232.--Fischer von Waldheim, 1821:72; 1828:250.--Mannerheim, 1843:189.--LeConte, 1863:2; 1878:473.--Motschulsky, 1846:128; 1850:72; 1860:98.--Sturm, 1826:173.

<u>Alpaeus</u> <u>gregarius</u> (Fischer von Waldheim).--Motschulsky, 1865:273.

<u>Nebria</u> <u>cuneata</u> Casey, 1913:50. LECTOTYPE (designated by Lindroth, 1975:111), a male, in USNM, labelled: "Alask"/ "Casey bequest 1925"/ "Type USNM 46851" [red label]/ "cuneata Csy."/ "Lectotype cuneata Csy. By C. H. Lindroth." TYPE LOCALITY.--

Alaska; here restricted to Unalaska Island, Aleutian Islands, Alaska.--Csiki, 1927:357.--Leng, 1920:46.--Lindroth, 1961a:66; 1975:111.

Nebria gregaris Van Dyke, 1924:4 [a misspelling].

Notes on nomenclature and types.--Fischer (1821:73) indicated that his description of N. gregaria was based on material in his own and Eschscholtz's collections. I have been unable to locate any Eschscholtz specimens of N. gregaria from among those in UMHF. Apparently, the single Fischer specimen (ZMUM) chosen as lectotype is the only survivor from the type series.

3.434132 Nebria charlottae Lindroth

(Figures 16, 68, 128, 142, 185, 393)

Nebria charlottae Lindroth, 1961a:67. HOLOTYPE, a male, in CNC, labelled: "Q. C. I. Kean"/ "Holotypus charlottae Lth." [red label]/ "Holotype No. 7611" [red label]. TYPE LOCALITY.--Queen Charlotte Islands, British Columbia.--de Ruette, 1970:15.

3.43414 The arkansana subgroup

3.434141 Nebria arkansana Casey

Nebria arkansana arkansana Casey

(Figures 193, 392)

Nebria eschscholtzii; auctorum (not Menetries).--Armin, 1963:89.--Wickham, 1902:232.

Nebria arkansana Casey, 1913:52. LECTOTYPE (designated by Lindroth,

1975:11), a male, in USNM, labelled: "Ind"/ "Casey bequest 1925"/ "Type USNM 46858" [red label]/ "arkansana Csy."/ "Lectotype arkansana Csy. BY C. H. Lindroth." TYPE LOCALITY:--Valley of the Upper San Juan River, Archuleta County, Colorado (designated by Lindroth, 1961a:70).--Armin, 1963:88.--Casey, 1924:21.--Csiki, 1927:367.--Leng, 1920:47.--Lindroth, 1961a:70 (in part); 1975:11.

Nebria sahlbergi; auctorum.--Armin, 1963:94.--Hatch, 1939a:120 (in part).--Lavigne, 1977:46.

Notes on nomenclature and types.--Lindroth was certainly correct in denying the validity of Casey's records for Arkansas and Indiana; and his choice for the new type locality is quite reasonable. The specimens in Casey's series are labelled "Ind" and "S. Ark"; and it is at least possible that the latter refers to the South Arkansas River (a quite suitable locality in Chaffee County, Colorado) rather than to the State of Arkansas as supposed by Casey.

Nebria arkansana edwardsi Kavanaugh, NEW SUBSPECIES

(Figures 147, 250, 268, 307, 331, 392)

Nebria sahlbergi; auctorum.--Edwards, 1975:48.--Mank, 1934:74.

Nebria arkansana; Lindroth, 1961a:70 (in part).

Nebria arkansana edwardsi, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Mont., Glacier N. P., Livingstone Range, Logan Pass Area, ne. slope Mt. Clements, 7100', 17July72 DHKavanaugh & JGEdwards"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria arkansana edwardsi Kavanaugh det.

D. H. Kavanaugh" [red label]/ "California Academy of Sciences Type No. 12495". Allotype (same data as holotype) also in CAS. 1861 paratypes (see Appendix B for locality data) are deposited in the following collections: AMNH, ANSP, BFCa, CAS, CNC, CUIC, DBUM, DHKa, DJLa, FMNH, INHS, JSch, JVMa, KUSM, LRus, MCZ, MSU, OSUO, PMNH, PURC, ROM, RTBe, SJSC, UAFA, UASM, UBC, UIMI, USNM, UWBM. TYPE LOCALITY.--Logan Pass, Glacier National Park, Montana.

Derivation of taxon name.--I take great pleasure in naming this subspecies in honor of J. Gordon Edwards, whose interest in life at high altitudes has fostered my own.

Nebria arkansana oowah Kavanaugh, NEW SUBSPECIES

(Figures 269, 332, 392)

Nebria arkansana oowah, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Utah, Grand Co., LaSal Mts., Mill Cr. at Oowah Lk., 8800', 2August71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria arkansana oowah Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12496". Allotype (same data as holotype) also in CAS. 75 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, MCZ, UASM, USNM. TYPE LOCALITY.--Mill Creek (at Oowah Lake) Grand County, Utah.

Derivation of taxon name.--This subspecies is named for the small, sheltered lake at the type locality.

Nebria arkansana uinta Kavanaugh, NEW SUBSPECIES

(Figures 30, 132, 194, 270, 392)

Nebria arkansana uinta, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Utah, Summit Co., Uinta Mts., Hwy. 150, Lost Lk., 9800', 14Aug71 DHKavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria arkansana uinta Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12497". Allotype (same data as holotype) also in CAS. 92 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, MCZ, UASM, USNM. TYPE LOCALITY.--Lost Lake, Summit County, Utah.

Derivation of taxon name.--This subspecies is named for the Uinta Mountains, in which the type locality is found.

3.434142 Nebria fragilis Casey

Nebria fragilis fragilis Casey

(Figures 126, 188, 224, 271, 394)

Nebria mannerheimii; Putnam (not Fischer von Waldheim), 1876b:199.

Nebria fragilis Casey, 1924:21. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "North Fork Provo Cañon IX-1 [?] Spalding"/ "Casey bequest 1925"/ "type USNM 46857" [red label]/ "Lectotype fragilis Csy. By C. H. Lindroth". TYPE LOCALITY.--North Fork Provo Canyon, Utah County, Utah.--Csiki, 1927:367.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:72;

1975:112.

Nebria fragilis teewinot Kavanaugh, NEW SUBSPECIES

(Figures 209, 394)

Nebria fragilis teewinot, new subspecies. HOLOTYPE, a male, in CAS labelled: "U.S., Wyo., Teton N. P., Teton Mts., Mt. Teewinot, stream on se. slope, 7100'-9000', 3Aug.73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria fragilis teewinot Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12500". Allotype (same data as holotype) also in CAS. 377 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, KUSM, MCZ, SJSC, UASM, USNM. TYPE LOCALITY.--Mount Teewinot (southeast slope), Grand Teton National Park, Wyoming.

Derivation of taxon name.--This subspecies is named for the type locality.

3.434143 *Nebria zioni* Van Dyke

Nebria zioni zioni Van Dyke

(Figures 31, 80, 99, 321, 394)

Nebria zioni Van Dyke, 1943:20. HOLOTYPE, a male, in CAS, labelled "Zion Canon, V-29-1935 Ut."/ "Van Dyke Collection"? "Holotype No. 5299 Nebria zioni Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 5299". Allotype (same data as

holotype) also in CAS (California Academy of Sciences Type No. 5300). TYPE LOCALITY.--Zion Canyon, Zion National Park, Utah.--Blackwelder and Blackwelder, 1948:2.--Lindroth, 1961a:72. --Tanner, 1928:269 (as "Nebria sp.").

Nebria zioni oasis Kavanaugh, NEW SUBSPECIES

(Figures 32, 212, 287, 394)

Nebria zioni oasis, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Utah, Washington Co., Pine Valley Mts., Leeds Cr. at Oak Grove Cmpgd., 6300'-6500', 20June71 DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria zioni oasis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12518". Allotype (same data as holotype) also in CAS. 46 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, MCZ, UASM, USNM. TYPE LOCALITY.--Leeds Creek (at Oak Grove Campground), Washington County, Utah.

Derivation of taxon name.--This subspecies is named for the oasis-like nature of the type locality--a spot of green, as it were, in an otherwise dry land.

3.4342 The obliqua group

This group is represented by six extant species, two of which (N. altaica and N. ochotica [including, for the present, N. japonica]) are restricted to central and eastern Asia, respectively. The

remaining species are endemic to North America--two restricted to eastern North America, one to the West, and one shared between both areas. (Fig. 420) The group includes taxa previously assigned to Lindroth's (1961a) "obtusa", "pallipes" (in part), and "appalachia" groups.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: head markedly shiny; pronotum with basal sinuation of lateral margin moderately long (except short in *N. suturalis* adults), width of lateral explanation medium or broad (except narrow in *N. appalachia* members); male genitalia: median lobe with mid-shaft markedly narrowed apically, shape (in cross-section) moderately or markedly compressed, ventral margin of preapical-shaft (lateral aspect) moderately recurved, apex (ventral aspect) narrowly pointed; female genitalia: bursa copulatrix with spermathecal chamber (dorsal aspect) round, insertion of spermathecal duct posterior/middle.

3.43421 The *obliqua* subgroup

3.434211 The *obliqua* infragroup

3.4342111 *Nebria suturalis* LeConte

(Figure 100, 159, 180, 313, 398)

Nebria suturalis LeConte, 1850:209. LECTOTYPE (here designated), a male, in MCZ, labelled: [light green disc]/ "Type 650" [red label]/ "suturalis 3"/ "Lectotype Nebria suturalis LeConte designated by D. H. Kavanaugh 1976" [red label]. Two female

paralectotypes (same data as lectotype) also in MCZ. TYPE LOCALITY.--Islands at mouth of Black Bay, Lake Superior, Ontario.--Bänninger, 1925:259.--Beaulne, 1914:30.--Blatchley, 1910:52.--Bowditch, 1896:2.--Casey, 1920:150.--Csiki, 1927:367. --Darlington, 1943:60.--Evans, 1906:96 (cannot refer to this species, but otherwise uninterpretable).--Gemminger and Harold, 1868:52.--Hatch, 1953:59.--Henshaw, 1881:206; 1885:4.--Horn, 1870:101.--Knobel, 1895:9.--Larochelle, 1975:95; 1977:112.--LeConte, 1863a:2; 1878:476.--Leng, 1920:47 (in part).--Lindroth, 1954b:122; 1961a:73; 1963a:76; 1975:112.--Melsheimer, 1853:11--Schaupp, 1878:45.

Nebria longula Le Conte, 1878:478. HOLOTYPE, a male, in MCZ, labelled: "Col."/ "Type 644" [red label]/ "N. longula LeC."/ "Holotype Nebria longula LeConte det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Colorado; here restricted to Longs Peak, Rocky Mountain National Park, Colorado. NEW SYNONYMY.--Armin, 1963:92 (in part).--Casey, 1920:150.--Csiki, 1927:364.--Henshaw, 1881:206; 1885:4.--Leng, 1920:47.--Lindroth, 1961a:73; 1969d:1109.--Schaupp, 1878:45.--Wickham, 1902:232.

Nebria nimbosa Casey, 1920:150. HOLOTYPE, a female, in USNM, labelled: "Lake of the Clouds Mt. Washington"/ "Casey bequest 1925"/ "Type USNM 46860" [red label]/ "nimbosa Csy."/ "Holotype nimbosa Csy. By C. H. Lindroth". TYPE LOCALITY.--Lake of the Clouds, Mount Washington, Coos County, New Hampshire.--Bänninger, 1925:259.--Csiki, 1927:367.--Larochelle, 1975:95.--

Leng and Mutchler, 1927:8.--Lindroth, 1954b:122; 1961a:73; 1975:112.

Nebria obtusa; Haubold (not LeConte), 1951:691 (in part).

3.4342112 Nebria obliqua Le Conte

(Figures 69, 101, 200, 216, 220-221, 343, 357, 395)

Nebria obliqua Le Conte, 1866:363. LECTOTYPE (here designated), a male, in MCZ, labelled: "Col."/ "Type 646" [red label]/ "Nebria obliqua Lec. Lewis Col."/ "obliqua 2"/ "Lectotype Nebria obliqua LeConte designated by D. H. Kavanaugh 1976" [red label]. One female paralectotype (same data as lectotype (also in MCZ. TYPE LOCALITY.--Colorado; here restricted to North Fork South Platte Canyon (at Santa Maria), Park County, Colorado.--Armin, 1963:92.--Casey, 1913:47.--Csiki, 1927;364.--Fall and Cockerell, 1907:156.--Gemminger and Harold, 1968:51.--Henshaw, 1881:206; 1885:4.--Horn, 1870:100.--Kirk and Balsbaugh, 1975:14.--Lavigne, 1977:46.--LeConte, 1878:476; 1879:500.--Leng, 1920:47.--Lindroth, 1961a:73; 1975:112.--Schaupp, 1878:45.--Van Dyke, 1926:10.--Wickham, 1902:231.

Nebria obtusa LeConte, 1878:478. HOLOTYPE, a male, in MCZ, labelled: "6-7,000 ft. Green River City, Wyo. July 2-27, 1877"/ "Type 647" [red label]/ "N. obtusa LeC."/ "Holotype Nebria obtusa LeConte det D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Green River City, Sweetwater County, Wyoming. NEW SYNONYMY.--Armin, 1963:92.--Bänninger, 1925:259; 1947:147.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:53.--Csiki,

1927:364.--Edwards, 1975:49.--Hatch, 1933:7; 1939:121; 1953:59. --Haubold, 1951:691 (in part).--Henshaw, 1881:206; 1885:4.--Kirk and Balsbaugh, 1975:14.--LeConte, 1879:500.--Leng, 1920:47. --Lindroth, 1961a:72; 1975:112.--Schaupp, 1878:45.--Spence, 1974:7.--Van Dyke, 1926:10.--Wickham, 1902:231.

Nebria mannerheimii; Wickham (not Fischer von Waldheim), 1902:231.

Nebria incerta Casey, 1913:53. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Col."/ "Casey bequest 1925"/ "Type USNM 46859" [red label]/ "incerta Csy."/ "Lectotype incerta Csy. By C. H. Lindroth". TYPE LOCALITY.--Colorado: here restricted to North Fork South Platte Canyon (at Santa Maria), Park County, Colorado.--Csiki, 1927:360.--Leng, 1920:47.--Lindroth, 1961a:73; 1975:112.

Nebria testaceipes Casey, 1913:54. HOLOTYPE, a male, in USNM, labelled: Glenora, B. C. Wickham."/ "Casey bequest 1925"/ "Type USNM 46861" [red label]/ "testaceipes Csy."/ "Holotype testaceipes Csy. By C. H. Lindroth". TYPE LOCALITY.--Glenora, British Columbia.--Beaulne, 1914:31.--Csiki, 1927:367.--Fall, 1926:130.--Hatch, 1953:59.--Leng, 1920:47.--Lindroth, 1961a:72; 1975:112.

Nebria texana Casey, 1913:54. HOLOTYPE, a male, in USNM, labelled: "Tex."/ "Casey bequest 1925"/ "Type USNM 46863" [red label]/ "texana Csy."/ "Holotype texana Csy. BY C. H. Lindroth". TYPE LOCALITY.--Texas.--Csiki, 1927:367.--Leng, 1920:47.--Lindroth, 1961a:73; 1975:112.

Nebria eschscholtzii; Beaulne (not Menetries), 1914:30.

Nebria _escholtzi_; auctorum.--Clark, 1948:25.--Hatch, 1933:7.

Nebria _longula_; Armin (not LeConte), 1963:92 (in part).

Notes on nomenclature and types. The type locality of _N. obliqua_, as originally stated, was Colorado. LeConte subsequently (1878:478) listed "North Fork of South Platte Cañon (7,000 to 8,000 ft.)" as a locality for the species; and Lindroth (1961a:73) accepted this as the type locality. I here formally restrict the type locality to this area.

My interpretation of LeConte's original description of _N. obtusa_ (1878:478-479) is that it is based on a single specimen (see p. 479, lines 7-8). I therefore list the type specimen as a holotype.

The holotype of _N. texana_ bears the label "Tex", interpreted by Casey as referring to the State of Texas (a highly improbable record). It is more probable the specimen was collected in Colorado, perhaps at Texas Creek (on the Arkansas River), Fremont County, Colorado. However, I have chosen not to amend or restrict the type locality pending further field search in the mountainous regions of western Texas.

3.434212 The _pallipes_ infragroup

3.4342121 _Nebria appalachia_ Darlington

(Figures 9, 17, 59, 102, 127, 183, 228, 257, 397)

Nebria _appalachia_ Darlington, 1931b:153. HOLOTYPE, a male in MCZ, labelled: "Smoky Mts. N.C.-Tenn. Newfound Gap 5,000-5,200 ft."/ "Aug. 30, 1930 Darlington"/ "Holotype Nebria appalachia Darl.

M.C.Z. 16433" [red label]. Allotype (same data as holotype) also in MCZ. TYPE LOCALITY.--Newfound Gap (naer 1520m), Great Smoky Mountains National Park, Tennessee.--Bell, 1955:265.--Csiki, 1933:631.--Fattig, 1949:12.--Leng and Mutchler, 1933:79.--Lindroth, 1961a:77.--de Ruette, 1970:15.

3.43421222 Nebria pallipes Say

(Figures 50, 103, 166, 201, 237, 351, 396)

Nebria pallipes Say, 1823:78. NEOTYPE (selected by Lindroth and Freitag, 1969:333), a male, in MCZ, labelled: "C. H. Frost Monterey"/ "Mass. Aug. 1, '20"/ "pallipes Say ♂"/ "C. A. Frost Collection 1962"/ "Neotypus Nebria pallipes Say design. Lth." [red label]. TYPE LOCALITY.--Massachusetts, Boston (county unspecified) (designated by Lindroth, 1961a:76).--Bänninger, 1925:260; 1949:147.--Beaulne, 1914:30.--Bell, 1955:265; 1967:104.--Blatchley, 1910:53.--Bowditch, 1896:2.--Casey, 1913:47.--Chagnon, 1914:167.--Csiki, 1927:365.--Darlington, 1931b:154.--Dillon and Dillon, 1961:67.--Fattig, 1949:12.--Gemminger and Harold, 1868:51.--Henshaw, 1885:4.--Horn, 1870:104.--Jeannel, 1937:4.--Kirk, 1970:9.--Knobel, 1895:9.--Larochelle, 1975:74; 1977:112.--LeConte, 1848:447; 1850:209; 1863a:2; 1878:477 (in part).--Leng, 1920:47.--Leonard, 1928:211.--Lindroth, 1954a:301; 1961a:76; 1963a:65; 1969:1149d.--Lindroth and Freitag, 1969:333.--Löding, 1945:12.--Melsheimer, 1853:11.--Provancher, 1877:148.--Schaupp, 1878:45.--Scudder, 1900:17.--Smith, 1910:200.--Spence, 1974:6.--Spence, Bell, and

Bell, 1976:81.--Spence and Bell, unpublished manuscript.--Sturm, 1843:16.--Ulke, 1902:6.

Nebria mühlenbergii Sturm, 1826:173 [here emended to Nebria muehlenbergii Sturm]. NOMEN NUDUM.--Csiki, 1927:365.--Gemminger and Harold, 1868:51.--Sturm, 1843:16.

Notes on nomenclature and types.--Lindroth (1969a:1149, and in Lindroth and Freitag, 1969:326) discusses the problem of establishing the actual publication date of Say's paper in which the original description of N. pallipes appeared. His comments support the date presented above rather than 1825 (as presented in Lindroth, 1961a:76).

Sturm (1843:16) cited N. muehlenbergii Sturm as a synonym of N. pallipes, thereby providing the only clue to his application of the name to a taxon.

3.4343 The mannerheimii group

This group is represented by six extant species, all endemic to western North America (Fig. 417). With exception of the three new or recently described species, the group is identical to Lindroth's (1961a) "mannerheimi" group.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: head moderately dull; pronotum with basal sinuation of lateral margin short, width of lateral explanation narrow; male genitalia: median lobe with mid-shaft markedly narrowed apically, shape (in cross section) moderately or markedly compressed, ventral margin of preapical-shaft (lateral aspect) faintly to moderately recurved,

apex (ventral aspect) narrowly pointed; female genitalia: bursa copulatrix with spermathecal chamber (dorsal aspect) spatulate or ovoid (slightly elongate longitudinally), insertion of spermathecal duct posterior/ventral.

3.43431 The mannerheimii subgroup

3.434311 Nebria darlingtoni Kavanaugh, NEW SPECIES (Figures 7, 104, 202, 316, 341, 399)

Nebria darlingtoni, new species. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., El Dorado Co., Sierra Nevada, S. F. American R., 3 mi. w. of Riverton, 910m, 16July75 D.H. & B.A. Kavanaugh Stop #75-29"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria darlingtoni Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12499". Allotype (same data as holotype) also in CAS. 170 paratypes (see Appendix B for locality data) are deposited in the following collections: AMNH, CAS, DHKa, ICCM, KSUC, KUSM, MCZ, UASM, USNM. TYPE LOCALITY.--South Fork American River (3 miles west of Riverton), El Dorado County, California.

Derivation of taxon name.--I take great pleasure in naming this species in honor of Philip J. Darlington, Jr., biogeographer, student of carabid evolution, and friend, whose work and encouragement have provided inspiration in this study.

3.434312 Nebria mannerheimii Fischer von Waldheim

(Figures 70, 105, 399)

Nebria mannerheimii Fischer von Waldheim, 1828:253. LECTOTYPE (here designated), a male, in ZMUM, labelled: "Sitcha"/ "48. mannerheimii Fisch"./ "Lectotype Nebria mannerheimii Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]. One male paralectotype in UMHF. TYPE LOCALITY.--Sitka, Baranof Island, Alaska.--Eschscholtz, 1833:23.--Hamilton, 1894:7.--Harrington, 1890:139.--Hatch, 1953:58.--Henshaw, 1885:4.--Horn, 1870:103.--LeConte, 1860:10; 1878:475.--Melsheimer, 1853:11.--Provancher, Schaupp, 1878:45.--Schwarz, 1900:524.--Taylor, 1886:35.--Van Dyke, 1919:4.--Wickham, 1893:213, 228.

Nebria mannerheimii Eschscholtz [an improper assignment of authorship]. --Dejean, 1831:575.--Fischer von Waldheim, 1828:253.--LeConte, 1863a:2; 1869:370.--Mannerheim, 1843:189.--Motschulsky, 1846:126; 1850:73.

Nebria mannerheimi; auctorum [unjustified emendation].--Bänninger, 1925:259.--Bates, 1883:218.--Beaulne, 1914:30.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:48; 1924:20.--Csiki, 1937:364. --Gemminger and Harold, 1868:51.--Hatch, 1933:7 (cannot refer to this species but otherwise uninterpretable); 1939a:120.--Jeannel, 1937:4.--Kavanaugh, 1971:44.--Leng, 1920:46.--Lindroth, 1961a:74; 1975:112.--Menetries, 1844:55.--Van Dyke, 1926:9; 1943:21.

Nebria sahlbergi; Keen, 1895:166.

Nebria gregaria; Schwarz (not Fischer von Waldheim), 1900:524 (in part).

Nebria oregona Casey, 1913:52. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "Clackamas Co. Oreg."/ "Casey bequest 1925"/ "Type USNM 46853" [red label2/ "oregona Csy."/ "Lectotype oregona Csy. By C. H. Lindroth". TYPE LOCALITY.--Clackamas Co., Oregon; here restricted to Zigzag River (at Rhododendron), Clackamas County, Oregon.--Csiki, 1937:364.--Hatch, 1953:58.--Leng, 1920:46.--Lindroth, 1961a:74; 1975:112.

Nebria corvallis Casey, 1924:20. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "Corvallis Or 7-4-12"/ "Casey bequest 1925"/ "Type USNM 46854" [red label]/ "corvallis Csy."/ "Lectotype corvallis Csy. By C. H. Lindroth". TYPE LOCALITY.--Corvallis, Benton County, Oregon.--Csiki, 1937:357. --Hatch, 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:74; 1975:112.

Nebria hippisleyi Casey, 1924:21. HOLOTYPE, a male, in USNM, labelled: "B. C. Terrace Hippisley"/ "Casey bequest 1925"/ "Type USNM 46868" [red label]/ "hippisleyi Csy."/ "Holotype hippisleyi Csy. By C. H. Lindroth". TYPE LOCALITY.--Terrace, British Columbia.--Blackwelder and Blackwelder, 1948:2.--Clark, 1948:25.--Csiki, 1937:388.--Hatch, 1939a:121; 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:74; 1975:112.

Notes on nomenclature and types.--Both specimens I recognize as comprising the type series of N. mannerheimii Fischer v. Wald. were

probably those collected by Eschscholtz (Fischer, 1828:253). The specimen chosen as lectotype is from the Fischer collection (ZMUM), the paralectotype is from the Mannerheim collection (UMHF) and bears an "Eschsch." label.

3.43432 The eschscholtzii subgroup

3.434321 The desolata infragroup

3.4343211 Nebria desolata Kavanaugh

(Figures 48, 71, 106, 143, 229, 272, 342, 400)

Nebria desolata Kavanaugh, 1971:41. HOLOTYPE, a male, in CAS, labelled: "Utah, Garfield Co., 11 mi. sw Boulder, The Gulch 5600' 16July69"/ [white dot]/ [red dot]/ [orange dot]/ "D. H. Kavanaugh Collector"/ "Holotype ♂ Nebria desolata D. Kavanaugh det. D. H. Kavanaugh 1969" [red label]/ "California Academy of Sciences Type No. 11388". Allotype (same as holotype) also in CAS. TYPE LOCALITY.--The Gulch (11 miles southwest of Boulder), Garfield County, Utah.

3.4343212 Nebria navajo Kavanaugh, NEW SPECIES

(Figures 195, 273, 400)

Nebria navajo, new species HOLOTYPE, a male, in CAS, labelled: "Kayenta Ariz. 19 mi sw VI-18-33"/ "Navajo Co. Alt. 6500 ft."/ "Ansel F Hall Exp. 1933"/ "H N Hultgren Collector"/ "Holotype Nebria navajo Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12509". One paratype (same data as holotype) also in CAS. TYPE LOCALITY.--Kayenta

(19 miles southwest), Navajo County, Arizona.

Derivation of taxon name.--This species is named for the people native to the region including the type locality.

3.434322 The eschscholtzii infragroup

3.4343221 Nebria eschscholtzii Ménétriés

(Figures 248, 274, 362, 400)

Nebria eschscholtzii Menetries, 1844:55. LECTOTYPE (here designated), a female, in ZILR, labelled: [gold-coated square]/ "California" [pink label]/ "Eschscholtzii Menet. Californ."/ "Syntypus" [red label]/ "Lectotype Nebria eschscholtzii Menetries designated by D. H. Kavanaugh 1976" [red label]. One paralectotype also in ZILR. TYPE LOCALITY.--California; here restricted to South Fork American River (3 miles west of Riverton), El Dorado County, California.--Hamilton, 1894:7 (in part; records from Alaska and British Columbia cannot refer to this species, but are otherwise uninterpretable).--Hatch, 1953:58.--Henshaw, 1881:206; 1885:4. --Horn, 1870:103.--LeConte, 1860:10; 1863a:2; 1878:475.--Motschulsky, 1846:128; 1850:72.--Schaupp, 1878:45.

Nebria castanipes; auctorum (not Kirby).--Hamilton, 1894:7.--Henshaw, 1881:206.--Horn, 1870:103 (in part).--LeConte, 1863:2 (in part). --Schaupp, 1878:46.

Nebria eschscholtzi; auctorum [unjustified emendation].--Bänninger, 1925:259; 1949:147.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:48; 1920:152.--Csiki, 1927:357.--Gemminger and

Harold, 1868:49.--Hatch, 1939:121.--Kavanaugh, 1971:44.--LaRivers, 1946:138.--Leng, 1920:46.--Lindroth, 1961a:75; 1975:112.--Van Dyke, 1926:9; 1943:21.

Nebria tenuipes Casey, 1913:51. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Alameda Co. Cal."/ "Casey bequest 1925"/ "Type USNM 468 2" [red label]/ "tenuipes Csy."/ "Lectotype tenuipes Csy. BY C. H. Lindroth". TYPE LOCALITY.--Alameda County, California; here restricted to Niles Canyon, Alameda County, California.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:367.--Hatch, 1939a:121; 1953:58.--Leng, 1920:46.--Lindroth, 1961a:75; 1975:112.

Nebria transversa Casey, 1920:152. HOLOTYPE, a female, in USNM, labelled: "Corvallis Or. 5-30-98"/ "Casey bequest 1925"/ "Type USNM 46869" [red label]/ "transversa Csy."/ "Holotype transversa Csy. By C. H. Lindroth". TYPE LOCALITY.--Corvallis, Benton County, Oregon.--Blackwelder and Blackwelder, 1948:2.--Casey, 1924:21.--Csiki, 1927:389.--Hatch, 1939a:121; 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nebria formalis Casey, 1920:153. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Wawawai Wash"/ "Casey bequest 1925"/ "Type USNM 46870" [red label]/ "formalis Csy."/ "Lectotype formalis Csy. By C. H. Lindroth". TYPE LOCALITY.--Wawawai, Whitman County, Washington.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:388.--Hatch, 1939a:121; 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nebria pallidissima Casey, 1924:19. LECTOTYPE (designated by Lindroth, 1975:112), a male, in USNM, labelled: "Wawawai Wash"/ "Casey bequest 1925"/ "Type USNM 46845" [red label]/ "pallidissima Csy."/ "Lectotype pallidissima Csy. By C. H. Lindroth". TYPE LOCALITY.--Wawawai, Whitman County, Washington.--Csiki, 1927:365.--Hatch, 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nebria pugetana Casey, 1924:19. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Wawawai Wash"/ "Casey bequest 1925"/ "Type USNM 46847" [red label]/ "pugetana Csy."/ "Lectotype pugetana Csy. By C. H. Lindroth". TYPE LOCALITY.--Wawawai, Whitman County, Washington.--Csiki, 1927:365.--Hatch, 1953:58.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nebria escholtzi Van Dyke, 1926:9 [a misspelling].

Nebria eschholtzi Jeannel, 1937:4 [a misspelling].

3.4343222 Nebria diversa LeConte

(Figures 8, 230-232, 306, 360, 401)

Nebria livida Le Conte, 1859a:84 [preoccupied by Carabus lividus Linnaeus, 1758:414]. LECTOTYPE (here designated), a male, in MCZ, labelled: [blue disc]/ "Type 642" [red label]/ "N. diversa LeC. livida|| LeC."/ "Lectotype Nebria livida LeConte designated by D. H. Kavanaugh 1976" [red label]. One paralectotype male (same data as lectotype) also in MCZ. TYPE LOCALITY.--Cape Flattery, Clallam County, Washington.--

Csiki, 1927:357.--Gemminger and Harold, 1868:49.--Hatch, 1953:59.--Henshaw, 1881:206.--LeConte, 1859b:287: 1863:2.--Leng, 1920:47.--Lindroth, 1961a:75.

Nebria diversa LeConte, 1863a:2 [as a replacement name for N. livida LeConte].--Bänninger, 1925:260.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:47: 1924:19.--Fletcher, 1906:100.--Gemminger and Harold, 1868:49.--Hatch, 1939:121; 1953:58.--Henshaw, 1881:206; 1885:4.--Horn, 1870:99.--Kavanaugh, 1971:45.--Keen, 1895:166.--LeConte, 1878:474.--Leng, 1920:47.--Lindroth, 1961a:75: 1975:112.--Schaupp, 1878:45.--Spence and Bell, unpublished manuscript.--Van Dyke, 1919:9; 1926:9.--Wickham, 1903:50.

Nebria townsendi Casey, 1924:19. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Port Townsend, Wash."/ "Casey bequest 1925"/ "Type USNM 46846" [red label]/ "townsendi Csy."/ "Lectotype townsendi Csy. By C. H. Lindroth". TYPE LOCALITY.--Port Townsend, Jefferson County, Washington.--Csiki, 1927:389.--Hatch, 1953:59.--Leng and Mutchler, 1927:8.--Lindroth, 1961a:75; 1975:112.

Nevria diversa Guppy, 1947:51 [a misspelling].

3.435 The *metallica* lineage

This lineage is represented by 18 extant species, three of which (namely, *N. mellyi* Gebler, *N. nitidula* (Fabricius), and *N. aenea* Gebler) are restricted to central and/or eastern Asia. The remaining species are endemic to western North America. Included in this lineage are taxa previously assigned to Lindroth's (1961a) "*metallica*," "*trifaria*," "*ingens*," and "*ovipennis*" groups, or to subgenus *Catonebria* Shilenkov (1975a).

Diagnostic combination.--Adult members of this lineage can be recognized by the following combination of character states: frontal red spot(s) present; paraglossae indistinct, completely fused with ligula; pronotum moderately to markedly cordate, midlateral pronotal setae present; hind coxa with two or more pairs of setae at base; ventroapical margin of fourth hind tarsomere projected, lobate; second through fifth visible abdominal sterna each with one or more pairs of anterior paralateral setae (except for *N. ovipennis* members); male genitalia: median lobe with basal bulb quadrate, broadly open basally, mid-shaft axis bent less than 135°, apex (ventral aspect) pointed; dorsobasal piece present as thin collar on basal bulb; female genitalia: basal apodeme of eighth sternum moderately to deeply emarginate, lateral arm not, moderately, or markedly shortened; proctiger hemispheric, heavily sclerotized throughout; medial area of valvifer membranous; coxite with setae of ventral diagonal row setiform; stylus with setae of mediodorsal row setiform, mediodorsal row longitudinal; bursa copulatrix with or without sclerite in dorsal wall of spermathecal chamber.

[illegible]

3.4351 The *ovipennis* group

This species group is represented by six extant species, one of which (*N. mellyi*) is restricted to the Altai Mountains (central Asia) and vicinity (Fig. 419). The group includes taxa previously assigned to Lindroth's (1961a) "*metallica*" (in part only) and "*ovipennis*" (excluding *N. paradisi*) groups.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: overall size medium or small; tooth of epilobe of mentum minute; second visible abdominal sternum with a pair of paramedial setae or with sparsely scattered setae medially; male genitalia: right dorsal face of median lobe mid-shaft faintly indented or more or less deeply invaginated to form a pouch; right medial parameric sclerite absent; female genitalia: spermathecal chamber (except in *N. carri* members) with a single, short to long and slender accessory lobe in midline on dorsum, ventral to spermathecal duct insertion; spermathecal duct medium length, loosely and unevenly convoluted.

3.43511 The *gebleri* subgroup

3.435111 *Nebria gebleri* Dejean

Nebria gebleri gebleri Dejean

(Figures 18, 107, 275, 318, 333, 402)

Nebria gebleri Dejean, 1831:573. HOLOTYPE, a female, in MHNP, labelled: "Sitka"/ "Gebleri Eschs"/ "Ex Musaeo Mniszech"/ "Holotype Nebria gebleri Dejean det. D. H. Kavanaugh 1976" [red

label]. TYPE LOCALITY.--shores of Sitka Sound ["Norfolk Sound"], Baranof Island, Alaska.--Bänninger, 1925:258.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:51.--Csiki, 1927:358.--Edwards, 1975:49.--Erwin and Ball, 1972:89.--Eschscholtz, 1833:23.--Fall, 1926:130.--Fletcher, 1904:95.--Gemminger and Harold, 1868:49.--Hamilton, 1894:7.--Hatch, 1939a:118 (in part); 1949:115; 1953:57.--Henshaw, 1885:4.--Horn, 1870:101.--Jeannel, 1937:4.--Kavanaugh and Martinko, 1972:147.--LeConte, 1860:10; 1863a:2; 1878:476.--Leng, 1920:46.--Lindroth, 1955b:12; 1961a:83 (in part).--Mank, 1934:74.--Melsheimer, 1853:11.--Schaupp, 1878:45.--Van Dyke, 1925:119 (in part); 1926:10 (in part).--Venables, 1913:268.

Nebria gebleri Eschscholtz [an improper assignment of authorship].--Dejean, 1831:573.--LeConte, 1860:10.--Mannerheim, 1843:188.--Motschulsky, 1850:73.

Nebria purpurata; auctorum (not LeConte).--Hatch, 1939a:119 (in part); 1953:58 (in part).--Lindroth, 1961a:86 (in part).--Mank, 1934:74.

Nebria melanaria Hatch, 1949:115. HOLOTYPE, a male, in UWBM, labelled: "G.N.P., Going-to-the-Sun Chalet, Aug. 26, 1939, M. H. Hatch"/ "Type ♂ Nebria melanaria M.H. Hatch 1948." TYPE LOCALITY.--Going-to-the-Sun Chalet, Glacier National Park, Montana.--Hatch, 1953:57.--Lindroth, 1961a:83.

Notes on nomenclature and types.--It is clear from his original description that the specimen of N. gebleri seen by Dejean was at that time complete. Lindroth (1955b:12), in his review of the

Dejean types, noted that the head and prothorax of the type specimen had been lost. In my study of the type, I now find it to be complete again. Unfortunately, the parts replaced are not only from a different specimen but from one representing a different species [=_Nebria picicornis_ (Fabricius)]. There is no doubt, however, that the pterothorax and abdomen (through which the pin passes) are the remains of the valid type specimen.

I have not seen the specimen from Boulder County, Colorado, which Armin (1961:89) identified as _N. gebleri_. The record is most improbable; and the specimen could have been either a small specimen of _N. pupurata_ LeC. or an unusually brilliant specimen of N. _arkansana arkansana_ Casey.

Nebria gebleri cascadensis Kavanaugh, NEW SUBSPECIES

(Figures 108, 402)

Nebria gebleri; auctorum.--Hatch, 1939a:118 (in part).--Lindroth, 1961a:83 (in part).--Van Dyke, 1925:119 (in part); 1926:10 (in part).

Nebria gebleri cascadensis, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Mt. Rainier N. P., Paradise R. above Narada Falls, 4580'-4800', 8Aug72 DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gebleri cascadensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12502." Allotype (same data as holotype) also in CAS. 1688 paratypes (see Appendix B for locality data) are deposited in the

following collections: AMNH, ANSP, BFCa, CAS, CNC, CUIC, DHKa, DJLa, FMNH, ICCM, INHS, JSch, KSUC, KUSM, LRus, MCZ, MSU, NMDo, ODa, OSUC, OSUO, PURC, ROM, RTBe, SDSU, SJSC, UAFA, UASM, UCB, UCR, UIMI, UMMZ, USNM, UWBM, UWEM, WSU. TYPE LOCALITY.--Paradise River (above Narada Falls), Mount Rainier National Park, Washington.

Derivation of taxon name.-- This subspecies is named for the Cascade Mountain Range, in which populations of this taxon are widely distributed.

Nebria gebleri rathvoni LeConte, NEW STATUS

(Figures 109, 402)

Nebria rathvoni LeConte, 1853:400. HOLOTYPE, a male, in MCZ, labelled: "6465 ft. Lake Tahoe, Cal. May 24, 1879"/ [light green square]/ "79." [red-tipped label]/ "N. rathvoni LeC."/ "Type 7403" [red label]/ "Holotype Nebria rathvoni LeConte det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Sacramento, California; here amended to Truckee River (at Truckee), Nevada County, California. NEW STATUS.--Bänninger, 1925:258.--Casey, 1913:51.--Csiki, 1927:367.--Gemminger and Harold, 1868:52.--Henshaw, 1881:206; 1885:4.--Horn, 1870:103.--LeConte, 1860:10; 1863:2.--Leng, 1920:46.--Lindroth, 1961a:83; 1969d:1109.--Schaupp, 1878:45.--Van Dyke, 1925:122.

Nebria rathvonii LeConte, 1878:475 [a misspelling].

Notes on nomenclature and types.--There is little reason to doubt that the specimen recognized above as the holotype is actually

the specimen seen by LeConte, although the specimen locality and date ("1879") label would indicate otherwise. It is the only specimen found in the LeConte Collection (MCZ). Because data on the first label conflict with the date (1853) and data of LeConte's original description, and because the label itself appears to be relatively new, I suspect that it has been more recently added to the original type specimen.

LeConte's type locality, Sacramento, is well outside the habitat range of the subspecies; so the type was surely not collected there. Truckee, as the amended type locality, is about at the midpoint of the habitat and geographical ranges of the subspecies.

Nebria gebleri siskiyouensis Kavanaugh, NEW SUBSPECIES

(Figures 110, 402)

Nebria gebleri siskiyouensis, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Calif., Trinity Co., Trinity Alps, S. F. Salmon R. at Big Flat Cmpgd., 1490m, 18July75 D. H. & B. A. Kavanaugh Stop #75-36"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gebleri siskiyouensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12503." Allotype (same data as holotype) also in CAS. 33 paratypes (see Appendix B for locality) are deposited in the following collections: CAS, DHKa, FMNH, UASM, USNM. TYPE LOCALITY.--South Fork Salmon River (at Big Flat Campground), Trinity County, California.

Derivation of taxon name.--This subspecies is named for the Siskiyou Mountains, in which members of this taxon were first

collected.

<u>Nebria gebleri strawberriensis</u> Kavanaugh, NEW SUBSPECIES

(Figures 110A, 276, 334, 402)

<u>Nebria gebleri strawberriensis</u>, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Ore., Grant Co., Blue Mts., Strawberry Cr., 5800' 28 May 1971, DHKavanaugh & EAMartinko"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria gebleri strawberriensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12501." Allotype (same data as holotype) also in CAS. 27 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, UASM, USNM. TYPE LOCALITY.--Strawberry Creek (1770m), Grant County, Oregon.

<u>Derivation of taxon name</u>.--This subspecies is named for the Strawberry Range of the Blue Mountains, to which it is apparently geographically restricted.

3.43512 The <u>ovipennis</u> subgroup

3.435121 The <u>kincaidi</u> infragroup

3.4351211 <u>Nebria carri</u> Kavanaugh, NEW SPECIES

(Figures 72, 111, 239, 277, 304, 405)

<u>Nebria carri</u>, new species. HOLOTYPE, a male, in CAS, labelled: "U.S.,Ida.,Blaine Co., Sawtooth Mts., Smoky Range, 2 mi. e. Dollarhide Summit, N. F. Warm Springs Creek, 7700'-7900',

21 Aug.73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria carri Kavanaugh, det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12498." Allotype (same data as holotype) also in CAS. 151 paratypes (see Appendix B for locality data) have been distributed among the following collections: BFCa, CAS, CNC, DHKa, FMNH, MCZ, UASM, USNM. TYPE LOCALITY.--Dollarhide Summit, Blaine County, Idaho.

Derivation of taxon name.--I take great pleasure in naming this species in honor of John and Betty Carr (Calgary, Alberta), who first collected specimens of same, and who have offered help and encouragement to me and other students in our respective studies.

3.4351212 Nebria kincaidi Schwarz

Nebria kincaidi kincaidi Schwarz

(Figures 73, 112, 149, 278, 335, 405)

Nebria kincaidi Schwarz, 1900:525. HOLOTYPE, a male, in USNM, labelled: "Farragut Bay, Alaska 6-5-99"/ "Harriman Expedition '99 T. Kincaid, Collector"/ "Nebria kincaidi Sz."/ "Type No. 56138 ♂ U.S.N.M." [red label]/ "Nebria kincaidi Schw. det. Schwarz Holotype." TYPE LOCALITY.--Farragut Bay, Alaska.--Bänninger, 1933:81; 1949:148.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2 (in part).--Csiki, 1927:369; 1933:630.--Darlington, 1930:104.--Erwin and Ball, 1972:85 (in part).--Hatch, 1939a:121 (in part); 1953:59.--Leng, 1920:46.--Lindroth, 1961a:88 (in part); 1975:113.--Perrault, 1972:62.--

Ueno, 1955:47.--Van Dyke, 1919:8 (in part); 1926:10.

Nebria columbiana Casey, 1913:48. LECTOTYPE (designated by Lindroth, 1975:113), a male, in USNM, labelled: "Inverness, B. Col."/ "Casey bequest 1925"/ "Type USNM 46848" [red label]/ "columbiana Csy."/ "Lectotype columbiana Csy. by C. H. Lindroth." TYPE LOCALITY.--Inverness, British Columbia.--Bänninger, 1925:265; 1933:81; 1949:148.--Beaulne, 1914:31.--Blackwelder, 1939:12.--Csiki, 1927:368; 1933:630.--Darlington, 1930:104.--Erwin and Ball, 1972:85.--Hatch, 1939a:121 (in part); 1953:59.--Leng, 1920:46.--Lindroth, 1961a:88; 1975:113.--Ueno, 1955:47.--Van Dyke, 1919:8 (in part); 1926:10 (in part).

Nebria paradisi; Clark (not Darlington), 1948:25.

Nebria kincaidi balli Kavanaugh, NEW SUBSPECIES

(Figures 150, 210, 405)

Nebria kincaidi; *auctorum*.--Blackwelder and Blackwelder, 1948:2 (in part).--Erwin and Ball, 1972:85 (in part).--Hatch, 1939:121 (in part).--Lindroth, 1961a:88 (in part).--Van Dyke, 1919:8 (in part).

Nebria columbiana; *auctorum* (not Casey).--Hatch, 1939a:121 (in part).--Van Dyke, 1919:8 (in part).

Nebria kincaidi balli, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S., Wash., Mt. Rainier N. P., Paradise R. above Narada Falls, 4580'-4800', 8Aug72, DHKavanaugh & HGoulet"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria kincaidi balli Kavanaugh det. D. H. Kavanaugh 1976" [red label]/

"California Academy of Sciences Type No. 12505." Allotype (same data as holotype) also in CAS. 358 paratypes (see Appendix B for locality data) have been distributed among the following collections: AMNH, CAS, CNC, CUIC, DHKa, FMNH, LACM, LRus, MCZ, MSU, ODA, OSUO, SJSC, UASM, USNM, UWBM, WSU. TYPE LOCALITY.--Paradise River (above Narada Falls), Mount Rainier National Park, Washington.

Derivation of taxon name.--I take great pleasure in naming this subspecies in honor of George E. Ball, my mentor and friend.

3.435122 The *ovipennis* infragroup

3.4351221 *Nebria spatulata* Van Dyke

Nebria spatulata spatulata Van Dyke

(Figures 20, 34, 74, 403)

Nebria spatulata Van Dyke, 1925:119. HOLOTYPE, a female, in CAS labelled: "Franklin Lake, Sept. 8"/ "M"/ "Type ♀ Nebria spatulata Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1625." TYPE LOCALITY.--Franklin Lake, Tulare County, California.--Blackwelder, 1939:12.--Csiki, 1927:389; 1933:631.--Darlington, 1930:105.--Erwin and Ball, 1972:83 (in part).--Leng and Mutchler, 1933:10.--Lindroth, 1961a:87.

Nebria fusiformis Van Dyke, 1926:11. NOMEN NUDUM.

Nebria spatulata sierrae Kavanaugh, NEW SUBSPECIES

(Figures 35, 190, 279, 403)

Nebria spatulata; Erwin and Ball, 1972:83 (in part).

Nebria spatulata sierrae, new subspecies. HOLOTYPE, a male, in CAS labelled: "U.S.A., Calif., Mono Co., Sierra Nevada Mts., ne. face White Mt., along streams in cirque above Big Horn Lake, 3290m-3480m, 21 July74 D.H.Kavanaugh Collector"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria spatulata sierrae Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12516." Allotype (same data as holotype) also in CAS. 58 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, MCZ, RPPa, UASM, UCB, USNM. TYPE LOCALITY.--White Mountain (east slope) above Big Horn Lake, Mono County, California.

Derivation of taxon name.--This subspecies is named for the Sierra Nevada, to which its geographical range is restricted.

3.4351222 *Nebria ovipennis* LeConte

(Figures 19, 33, 75, 243, 246, 280, 295, 404)

Nebria ovipennis LeConte, 1878:477. HOLOTYPE, a male, in MCZ, labelled: "Sierra Nev. Cal."/ "Type 648" [red label]/ "N. ovipennis *LeC*."/ "Holotype Nebria ovipennis LeConte det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Sierra Nevada, California; here restricted to Mount Conness (east slope, above Greenstone Lake),Mono County, California.--Bänninger, 1925:264;

1949:148.--Casey, 1913:47.--Csiki, 1927:370.--Darlington, 1930:104.--Erwin and Ball, 1972:81.--Henshaw, 1881:206; 1885:4.--Leng, 1920:46.--Lindroth, 1961a:87.--Papp, 1978:126.--Schaupp, 1878:45.--Schwarz, 1900:525.--Van Dyke, 1919:8; 1925:120; 1926:10.

Notes on nomenclature and types. The type specimen of *N. ovipennis* is representative of populations north of Mount Lyell, Yosemite National Park but not south of that point in the Sierra Nevada. The restricted type locality is therefore both more precise and appropriate for the form represented by the type specimen.

3.4352 The *metallica* group

This species group is represented by four extant species--two (namely, *N. aenea* Gebler and *N. nitidula* (Fabricius))restricted to eastern and/or central Asia, and two restricted to western North America (Fig. 421). Lindroth (1961a) assigned the Nearctic species to his "*metallica*" group.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: overall size medium; tooth of epilobe of mentum moderately long; second visible abdominal sternum asetose medially; male genitalia: right dorsal face of median lobe mid-shaft unmodified, convex; right medial parameric sclerite present; female genitalia: spermathecal chamber without dorsal accessory lobe(s) in midline; spermathecal duct slightly shortened, sinusoidal (i.e. evenly, regularly convoluted [Fig. 350]).

The only character in the above list by which all members of this group can be distinguished from members of the following (_trifaria_) group is, unfortunately, overall size. I have no doubt that this group is both a monophyletic assemblage and the sister of the _trifaria_ group. However, the distribution of character states among members of these two groups is so complex that even simple combinations of characters by which respective group members can be distinguished (=polythetic definitions) cannot be recognized at present. Such problems in definition can be expected occasionally when ranking is based on phylogenetic relationship rather than phenetic similarity. Review of data presented in Fig. 372 will demonstrate that recognition of this group as monophyletic and distinct from the _trifaria_ group provides the simplest explanation for the cumulative distribution of states of all characters.

3.43521 The _meanyi_ subgroup

3.435211 _Nebria meanyi_ Van Dyke

Nebria meanyi meanyi Van Dyke

(Figures 113, 151, 167, 406)

Nebria meanyi Van Dyke, 1925:118. HOLOTYPE, a male, in CAS, labelled: "Nesqually Riv. below glacier"/Mt. Rainier Wash. IX-5-1912"/ "Coll. by Elliott"/ "Van Dyke Collection"/ "Type ♂ Nebria meanyi Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1623." Allotype (same data as holotype) also in CAS (California Academy of Sciences Type No. 1624). TYPE LOCALITY.--Nisqually River (below toe of Nisqually Glacier),

Mount Rainier National Park, Washington.--Bänninger, 1931:178.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1927:388; 1933:631.--Hardy, 1927:C22.--Hatch, 1939a:118 (in part); 1953:57.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:84.--Van Dyke, 1926:10.

Nebria meanyi lamarckensis Kavanaugh, NEW SUBSPECIES

(Figures 114, 152, 211, 406)

Nebria meanyi lamarckensis, new subspecies. HOLOTYPE, a male in CAS, labelled: "U.S., Calif., Inyo Co., Sierra Nevada, Lamarck Cr. above Upper Lamarck Lk., 10700'-11000' 6July71 DHKavanaugh & EAMartinko"/ "71-248" [orange label]/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria meanyi lamarckensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12507." Allotype (same data as holotype) also in CAS. 21 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, DHKa, UASM, USNM. TYPE LOCALITY.--Lamarck Creek (above Upper Lamarck Lake), Inyo County, California.

Derivation of taxon name.--The name for this subspecies refers to the type locality, Lamarck Creek, which in turn refers to Jean Baptiste Pierre Antoine Lamarck, the noted French naturalist and pioneer evolutionist.

Nebria meanyi sylvatica Kavanaugh, NEW SUBSPECIES

(Figures 115, 406)

Nebria meanyi; Hatch, 1939a:118 (in part).

Nebria meanyi sylvatica, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Wash., Olympic N. P., Olympic Mts., Boulder Cr., at Olympic Hot Springs, 610m, 15Aug.74 D. H. Kavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria meanyi sylvatica Kavanaugh det. by D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12508." Allotype (same data as holotype) also in CAS. 177 paratypes (see Appendix B for locality data) are deposited in the following collections: CAS, CNC, CUIC, DHKa, ICCM, JSch, UASM, USNM, UWBM. TYPE LOCALITY.--Boulder Creek (at Olympic Hot Springs), Olympic National Park, Washington.

Derivation of taxon name.--This subspecies name is derived from the Latin word, *sylvaticus*, meaning "of the forest," and referring to the deep forest habitat occupied by taxon members.

3.43522 The *metallica* subgroup

3.435221 The *metallica* infragroup

3.4352211 *Nebria metallica* Fischer von Waldheim

(Figures 21, 116, 172, 222, 407)

Nebria metallica Fischer von Waldheim, 1821:71.

LECTOTYPE (here designated), a male, in ZMUM, labelled: "Unalaschka. F."/ "73 metallica Fisch."/ "Lectotype Nebria metallica Fischer v. Wald. designated by D. H. Kavanaugh 1977" [red label]. Two paralectotypes, one male and one female, are

in UMHF. TYPE LOCALITY.--Unalaska, Unalaska Island, Aleutian Islands, Alaska.--Bänninger, 1925:258; 1928:5; 1931:178; 1949:147.--Beaulne, 1914:29.--Blackwelder and Blackwelder, 1948:2.--Bush, 1914:59.--Casey, 1913:47.--Chaudoir, 1850:424.--Criddle, 1922:61.--Csiki, 1927:364; 1933:631.--Dejean, 1831:574.--Eschscholtz, 1823:100, 1833:23.--Fall, 1826:129.--Gemminger and Harold, 1868:51.--Hamilton, 1894:6.--Hatch, 1938:145; 1939a:118.--Henshaw, 1885:4.--Horn, 1870:100.--Jeannel, 1937:4.--LeConte, 1860:10; 1863:2; 1878:476.--Leng, 1920:46.--Lindroth, 1961a:84; 1963b:123.--Melsheimer, 1853:11.--Perrault, 1972:62.--Schaupp, 1878:45.--Schwarz, 1900:524.--Van Dyke, 1924:4; 1925:117; 1926:9; 1943:20.--Wickham, 1893:223, 228.

Nebria metallica Eschscholtz [an improper assignment of authorship].--Dejean, 1826:229.--Eschscholtz, 1823:100.--Fischer von Waldheim, 1821:71; 1828:245.--Mannerheim, 1843:188.--Motschulsky, 1850:73; 1865:273.--Sturm, 1826:173.

Nebria pacifica Chaudoir, 1850:424. HOLOTYPE, a female, in MHNP, labelled: "Otahiti ???"/ "pacifica Chaudoir"/ "Muséum Paris 1952 Coll R. Oberthür"/ "Holotype Nebria pacifica Chaudoir det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Tahiti, Society Islands, French Polynesia [doubtful record].--Bänninger, 1931:178.--Csiki, 1927:389; 1933:631.--Gemminger and Harold, 1868:51.--Lindroth, 1961a:85.

Nebria metallica metallica Fischer von Waldheim.--Hatch, 1953:57.

Notes on nomenclature and types.--Fischer's description of *metallica* was based on material in his own and in Eschscholtz's

collections (Fischer, 1821:72). Specimens from the latter, identified as such, are now in UMHF as part of the Mannerheim collection. I have chosen the Fischer specimen as lectotype, the two Eschscholtz specimens as paralectotypes. A fourth specimen, in the Fischer collection (ZMUM), bears a "Kadjak" [Kodiak] label and is thus excluded from the type series.

3.4353 The *trifaria* group

This species group is represented by eight extant species, all endemic to western North America (Fig. 418). Species included in this group were previously assigned to Lindroth's (1961a) "*metallica*," "*ingens*," and "*trifaria*" groups.

Diagnostic combination.--Adult members of this group can be recognized by the following combination of character states: overall size large or very large; tooth of epilobe of mentum moderately to very long; second visible abdominal sternum asetose medially; male genitalia: right dorsal face of median lobe mid-shaft unmodified, convex; right medial parameric sclerite present (except in *trifaria* infragroup members); female genitalia: spermathecal chamber without dorsal accessory lobe(s) in midline; spermathecal duct slightly shortened, sinusoidal (i.e. evenly, regularly convoluted [Fig. 350]). Refer to comments in section 3.4352 concerning the phenetic distinction between this and the *metallica* species group.

3.43531 The _ingens_ subgroup

3.435311 _Nebria_ _ingens_ Horn

Nebria _ingens_ _ingens_ Horn

(Figures 22, 43, 52, 63, 76, 117, 154, 242, 245, 408)

Nebria _ingens_ Horn, 1870:98. LECTOTYPE (here designated), a female, in MCZ, labelled: "Cala."/ "TypeNo. 1026" [red label]/ "Nebria ingens Horn"/ "Lectotype Nebria ingens Horn designated by D. H. Kavanaugh 1976" [red label]. One female paralectotype, also in MCZ, labelled: "Cala."/ "Type 8127" [red label]/ "N. ingens Horn." TYPE LOCALITY.--Sierra Nevada Mountains east of Visalia, California; here restricted to Franklin Lake, Tulare County, California.--Casey, 1913:47.--Csiki, 1927:369.--Darlington, 1930:105.--Erwin and Ball, 1972:80.--Henshaw, 1885:4.--LeConte, 1878:474.--Leng, 1920:46.--Lindroth, 1961a:87 (in part).--Schaupp, 1878:45.--Schwarz, 1900:525.--Van Dyke, 1919:8; 1925:116; 1926:11; 1953:102.

Nebria _raveni_ Van Dyke, 1953:102. HOLOTYPE, a female, in CAS, labelled: "stream from snow runoff, Mt. Darwin, 13600ft."/ Fresno Co. Calif. VIII-9-1952, Coll. by P. Raven"/ "Holotype ♀ Nebria raveni Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 8163." TYPE LOCALITY.--Mount Darwin (4150m), Fresno County, California.--Lindroth, 1961a:87.

Notes on nomenclature and types.--In his original description, Horn mentioned two specimens, a male and a female. The MCZ specimen seen by Lindroth (his "allotype," 1961:87) is a female. The other

specimen, from the Horn Collection (formerly at ANSP, now at MCZ), is also a female; so Horn did not actually see a male. The lectotype chosen for N. ingens is the specimen from the Horn Collection.

Nebria ingens riversi Van Dyke, NEW STATUS

(Figures 130, 408)

Nebria riversi Van Dyke, 1925:115. HOLOTYPE, a male, in CAS, labelled: "Mt. Lyell, Yosemite Pk. Cal. VII-13-1921"/ "Van Dyke Collection"/ "Type ♂ Nebria riversi Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1619." Allotype (same locality data as holotype) also in CAS (Type No. 1620). TYPE LOCALITY.--Mount Lyell (3440m), Yosemite National Park, California.--Allen, 1967:82.--Blackwelder, 1939:12.--Csiki, 1927:389; 1933:631.--Darlington, 1930:105.--Döbler, 1975:138.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:87.--Van Dyke, 1926, 1926:11; 1953:102.

Nebria ingens; Lindroth, 1961a:87 (in part).

3.435312 Nebria vandykei Bänninger

Nebria vandykei vandykei Bänninger

(Figures 36, 55, 160, 288, 408)

Nebria trifaria; Van Dyke (not LeConte), 1919:8 (in part); 1925:116 (in part); 1926:10 (in part).

Nebria vandykei Bänninger, 1928:5. LECTOTYPE (here designated), a male, in ETHZ, labelled: "Paradise Val. Mt. Rainier Wash. VII-18-1920"/ "Coll. by E. C. Van Dyke"/ "1. Fühl.gld. as.

1 + 2 B."/ "FG. Basig. bil. OP!"/ "Nebria trifaria LeC."/ "Type Nebria Van Dykei 10.1927" [red-trimmed label]/ "Lectotype Nebria vandykei Bänninger designated by D. H. Kavanaugh 1976" [red label]. Two paralectotypes also in ETHZ. TYPE LOCALITY.--Paradise Valley, Mount Rainier National Park, Washington.--Blackwelder and Blackwelder, 1948:2.--Csiki, 1933:630.--Darlington, 1931:24.--Erwin and Ball, 1972:87 (in part).--Hatch, 1939a:118 (in part); 1949:116.--Leng and Mutchler, 1933:11.--Lindroth, 1961a:86 (in part).--Mann, 1978:20.

Nebria trifaria vandykei Bänninger.--Hatch, 1953:56 (in part).

Notes on nomenclature and types.--In his original description of *N. vandykei*, Bänninger listed four specimens in the type series; but only three of these are accounted for at present (W. Sauter, personal communication).

Nebria vandykei wyeast Kavanaugh, NEW SUBSPECIES

(Figures 37, 218, 258-259, 408)

Nebria vandykei; auctorum.--Erwin and Ball, 1972:87 (in part).--Hatch, 1939a:118 (in part).--Lindroth, 1961a:86 (in part).

Nebria trifaria vandykei Bänninger.--Hatch, 1953:56 (in part).

Nebria vandykei wyeast, new subspecies. HOLOTYPE, a male, in CAS, labelled: "U.S.A., Ore., Clackamas Co., Cascade Range, s. slope Mt. Hood, headwaters Salmon R. near Timberline Lodge, 1830m-1950m, 3Aug.74 D. H. Kavanaugh"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria vandykei wyeast Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California

Academy of Sciences Type No. 12517." Allotype (same data as holotype) also in CAS. 186 paratypes (see Appendix B for locality data) are deposited in the following collections: CAS, DHKa, MCZ, OSUO, UASM, USNM, UWBM. TYPE LOCALITY.--Salmon River headwaters, Mount Hood, Clackamas County, Oregon.

Derivation of taxon name.--For this subspecies, I choose the name given to Mount Hood by local native peoples--*Wy'east*, which means "The Mountain."

3.43532 The *schwarzi* subgroup

3.435321 *Nebria piperi* Van Dyke

(Figures 118, 125A, 144, 153, 204, 208, 317, 350, 364, 409)

Nebria piperi Van Dyke, 1925:117. HOLOTYPE, a male, in CAS, labelled: "Nesqually Riv. below glacier"/ "Mt. Rainier Wash. IX-5-1912"/ "Coll. by Elliott"/ "Van Dyke Collection"/ "Type ♂ Nebria piperi Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 1621." Allotype, also in CAS, from Mount Baker, Washington (California Academy of Sciences Type No. 1622). TYPE LOCALITY.--Nisqually River (below toe of Nisqually Glacier), Mount Rainier National Park, Washington.--Bänninger, 1928:5; 1931:178.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Criddle, 1926:96.--Csiki, 1927:289; 1933:631.--Hatch, 1939a:119.--Leng and Mutchler, 1933:10.--Lindroth, 1961a:85.--Perrault, 1972:62.--Van Dyke, 1926:10.

Nebria metallica piperi Van Dyke.--Hatch, 1953:57.

3.435322 _Nebria_ _schwarzi_ Van Dyke

Nebria _schwarzi_ _schwarzi_ Van Dyke

(Figures 119, 161, 168, 205, 226, 409)

Nebria _schwarzi_ Van Dyke, 1925:116. HOLOTYPE, a male, in USNM, labelled: "Banff Sp 10.6 Alb."/ "Coll Hubbard & Schwarz"/ "U.S.N.M. Type No. 28174" [red label]/ "Type Nebria schwarzi VAn Dyke" [red-tipped label]. TYPE LOCALITY.--Banff, Banff National Park, Alberta.--Bänninger, 1928:5; 1931:178.--Blackwelder, 1939:12.--Blackwelder and Blackwelder, 1948:2.--Criddle, 1926:96.--Csiki, 1927:389; 1933:631.--Hatch, 1939:119.—Leng and Mutchler, 1933:10.--Lindroth, 1961a:86.--Van Dyke, 1926:10.

Nebria _metallica_ _schwarzi_ Van Dyke.--Hatch, 1953:57

Nebria _schwarzi_ _beverlianna_ Kavanaugh, NEW SUBSPECIES

(Figures 120, 227, 296, 409)

Nebria _schwarzi_ _beverlianna_, new subspecies, HOLOTYPE, a male, in CAS, labelled: "U.S., Wyo., Sublette Co., Gros Ventre Mts., Hwy. 187/189, 8 mi. nw. Bondurant, Hoback R., 6900', 1-2 August 73 DHKavanaugh Family"/ "D. H. Kavanaugh Collection" [orange label]/ "Holotype Nebria schwarzi beverlianna Kavanaugh det. D. H. Kavanaugh 1976" [red label]/ "California Academy of Sciences Type No. 12515." Allotype (same data as holotype) also in CAS. 253 paratypes (see Appendix B for locality data) have been distributed among the following collections: CAS, CNC,

DHKa, FMNH, HGou, MCZ, UASM, USNM. TYPE LOCALITY.--Hoback River (8 miles northwest of Bondurant), Sublette County, Wyoming.

Derivation of taxon name.--I take great pleasure in naming this subspecies in honor of my wife, Beverly Ann Kavanaugh.

3.43533 The *trifaria* subgroup

3.435331 The *purpurata* infragroup

3.4353311 *Nebria purpurata* LeConte

(Figures 42, 81 120A, 131, 187, 241, 244, 358, 49)

Nebria purpurata LeConte, 1878:477. HOLOTYPE, a male, in MCZ, labelled: "9-10,000 ft. Leavenworth Vall. ab. Georgetown, Col. July 14, 17, 1877"/ "Type 649" [red label]/ "N. purpurata LeC."/ "Holotype Nebria purpurata LeConte det. D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--Leavenworth Valley (2740m-3050m), Clear Creek County, Colorado.--Armin, 1963:93.--Bänninger, 1925:250.--Beaulne, 1914:29 (cannot refer to this species, but otherwise uninterpretable).--Blackwelder and Blackwelder, 1948:2.--Casey, 1913:49.--Csiki, 1927:367.--Erwin and Ball, 1972:89.--Fall and Cockerell, 1907:156.--Hatch, 1939:119; 1953:58 (in part).--Haubold, 1951:704.--Henshaw, 1881:206; 1885:4.--Kavanaugh and Martinko, 1972:147.--LeConte, 1879:500.--Leng, 1920:46.--Lindroth, 1961a:86 (in part); 1975:112.--Schaupp, 1878:45.--Van Dyke, 1925:116; 1926:10 1943:20.--Wickham, 1902:231.

Nebria mobilis Casey, 1913:50. LECTOTYPE (designated by Lindroth,

1975:112), a female, in USNM, labelled: "Col."/ "Casey bequest 1925"/ "Type USNM 46850" [red label]/ "mobilis Csy."/ "Lectotype mobilis Csy. By C. H. Lindroth." TYPE LOCALITY.--Colorado.--Csiki, 1927:364.--Erwin and Ball, 1972:89.--Leng, 1920:46.--Lindroth, 1961a:86; 1975:112.

3.435332 The trifaria infragroup

3.4353321 Nebria trifaria LeConte

Nebria trifaria trifaria LeConte

(Figures 38, 77, 121, 173, 281, 337, 411)

Nebria trifaria LeConte, 1878:478. LECTOTYPE (here designated), a male, in MCZ, labelled: "9500 ft. Amer. Fork Canon Utah, Aug. 2-3, 1877"/ "Type 651" [red label]/ "N. trifaria LeC."/ "Lectotype Nebria trifaria LeConte designated by D. H. Kavanaugh 1976" [red label]. TYPE LOCALITY.--American Fork Canyon (2900m), Utah County, Utah.--Armin, 1963:94.--Bänninger, 1925:258; 1928:5.--Blackwelder and Blackwelder, 1948:2.--Blake, 1945:237.--Casey, 1913:48; 1924:21.--Csiki, 1927:367.--Hatch, 1939a:118; 1949:116.--Henshaw, 1881:206; 1885:4.--Lavigne, 1977:46.--Leng, 1920:46.--Lindroth, 1961a:86.--Schaupp, 1878:45.--Van Dyke, 1919:8 (in part); 1925:116 (in part); 1926:10 (in part).--Wickham, 1902:232 (in part).

Nebria trifaria trifaria LeConte.--Erwin and Ball, 1972:93.--Hatch, 1953:57.

Nebria trifaria coloradensis Van Dyke.--Erwin and Ball, 1972:95 (in

part).

Nebria trifaria tetonensis Erwin and Ball, 1972:95. HOLOTYPE, a male, in USNM, labelled: "Teton Natl. Park, Wyo. 22 July 60"/ "S. Fk. Cascade Cyn. --10000 ft. snow --10:30 pm"/ "Alice Edwards J. G. Edwards"/ "6267"/ "2197"/ "♂ apex drawn Erwin 1970"/ "Holotype Nebria trifaria tetonensis Erwin and Ball USNM 71975" [red label]. Allotype (same data as holotype) also in USNM. TYPE LOCALITY.--South Fork Cascade Canyon (3050m), Grand Teton National Park, Wyoming. NEW SYNONYMY.

Nebria trifaria catenata Casey

(Figures 39, 78, 198, 282, 338, 411)

Nebria trifaria; Wickham, 1902:232 (in part).

Nebria catenata Casey, 1913:49. LECTOTYPE (designated by Lindroth, 1975:112), a female, in USNM, labelled: "Col"/ "Casey bequest 1925"/ "Type USNM 46849" [red label]/ "catenata Csy."/ "Lectotype catenata Csy. By C. H. Lindroth." TYPE LOCALITY.--Colorado; restricted by Erwin and Ball (1972:97) to San Juan Mountains, and here further restricted to Wolf Creek Pass, Mineral County, Colorado.--Csiki, 1927:357.--Leng, 1920:46.--Lindroth, 1961a:84 (in part).

Nebria trifaria catenata Casey.--Erwin and Ball, 1972:97.--Lindroth, 1975:112.

Nebria trifaria utahensis Kavanaugh, NEW SUBSPECIES

(Figures 121A, 196, 283, 339, 411)

Nebria trifaria utahensis, new subspecies. HOLOTYPE, a male, in CNC, labelled: "Lonesome Beaver, 7500', Henry Mts., Utah VII 20-22, 68 H. F. Howden"/ "Holotype Nebria trifaria utahensis Kavanaugh det. D. H. Kavanaugh 1976" [red label]. Allotype (same data as holotype) also in CNC. 13 paratypes (see Appendix B for locality data) deposited in the following collections: CAS, CNC. TYPE LOCALITY.--Lonesome Beaver, Henry Mountains, Garfield County, Utah.

Derivation of taxon name.--This subspecies is named for the State of Utah, in which its geographical range is restricted.

3.4353322 *Nebria coloradensis* Van Dyke

(Figures 40, 122, 184, 336, 4]0)

Nebria coloradensis Van Dyke, 1943:19. HOLOTYPE, a male, in CAS, labelled: "Twin Lakes Col. Lake Co. VI-26-35"/ "Van Dyke Collection"/ "Holotype No. 5298 Nebria coloradensis Van Dyke" [red-tipped label]/ "California Academy of Sciences Type No. 5298." TYPE LOCALITY.--Twin Lakes, Lake County, Colorado.--Blackwelder and Blackwelder, 1948:2.--Lindroth, 1961a:84.

Nebria catenata; Lindroth (not Casey), 1961a:84 (in part).

Nebria trifaria coloradensis Van Dyke.--Erwin and Ball, 1972:96 (in part).

3.4353323 Nebria piute Erwin and Ball, NEW STATUS

(Figures 41, 285, 336A, 410)

Nebria trifaria piute Erwin and Ball, 1972:95. HOLOTYPE, a male, in USNM, labelled: "Utah. Piute Co., LaBaron L., Circleville Mt., 15.9 mi. w. Junction 9700', Sept/ 17, 1967"/ "Ball, T. L. Erwin, R. E. Leech Collectors"/ "Holotype Nebria trifaria piute Erwin and Ball USNM 71976" [red label]. Allotype (same data as holotype) also in USNM). TYPE LOCALITY.--LaBaron Lake, Circleville Mountain, Beaver County, Utah. NEW STATUS.

4.0 ANALYSES OF THE NEARCTIC NEBRIA FAUNA

In this section, data from comparative morphological, chorological, and natural history studies presented above are used in phylogenetic and zoogeographic analyses of the Nearctic Nebria fauna. The classification provided in section 3.33 is based on these analyses.

4.1 Phylogeny

4.11 Introduction

I here present a phylogenetic classification of characters, a cladistic analysis of Nearctic Nebria taxa, and a cladogram which represents hypothetically, phylogenetic relationships among these taxa. As noted by Griffiths (1974a) and Kavanaugh (in press C), the primary goal of cladistic analysis is systematization (see definition and further discussion above, section 3.31) rather than classification. In my view, the relationship between systematization and classification is sequential--the latter follows from the former. The rationale behind and justification for use of cladistic techniques for recognition of systems and elucidation of relationships among their elements (i.e. systematization) has been explored in depth by Brundin (1972), Griffiths (1974a and 1974b), and Whitehead (1972). Because I agree with both presentations and conclusions of these authors, I here omit further theoretical review and simply present the procedures and assumptions used in the study of Nebria species.

Taxa as systems and as elements.--As noted in section 3.31, species are, necessarily, elements of natural systems produced by speciational processes of evolution. Correspondence between taxonomic groups (e.g. species groups) and natural systems is achieved only if a criterion of strict monophyly (sensu Hennig, 1966; ="holophyly" of Ashlock, 1974) is applied in recognition of the former. Monophyletic groups are defined as those which include a stem species (common ancestor) and only and all its descendants. Groups which include species with separate ancestry (i.e. polyphyletic groups) or from which one or more descendant species have been excluded (i.e. paraphyletic groups) are not systems at all or only incomplete ones, respectively. The objective of the cladistic analysis presented here was, therefore, recognition of strictly monophyletic groups (systems) of successively greater inclusiveness, from single species (element) pairs to an ultimate group comprising all members of the Nearctic fauna.

Degree of phylogenetic relationship is proportional to relative recency of common ancestry. For example, the phylogenetic relationship between two species, A and B (Fig. 367), is greater than between either and a third species, C, if and only if A and B have a common ancestor, D, not also shared with C. Taxa which share closest phylogenetic relationship are called "sister" taxa. As suggested by Hennig (1966), only possession of synapotypic (i.e. shared, derived) character states is evidence in support of close phylogenetic relationship, sister group status, or the monophyly of groups of any size. In the above example, evidence that species A and B are in fact closest relatives is obtained if their members demonstrate one or more synapotypic character states not also shared with members of species

C. The procedures outlined below are therefore directed toward recognition of sister taxa through a search for synapotypy.

Polarity and sequence of transformation series.--Recognition of synapotypy requires an existing classification of the states of a character as elements of a transformation series (i.e. an evolutionary sequence of homologous character states) (Hennig, 1966) arranged from most plesiotypic (i.e. primitive) to most apotypic (i.e. derived). Determination of this polarity is the critical phase of cladistic analysis; and hypotheses generated from these analyses are valid only to the extent that hypotheses on polarity and sequence of individual characters are accurate (i.e. reflect evolutionary history of the characters). If, in fact, we could know (with certainty) the polarity of series, reconstruction of phylogenetic relationships would be relatively simple. Because this certainty is unattainable, we must rely on criteria for and tests of hypotheses on polarity. Ball (1975), Ekis (1977), Platnick (1977), and Ross (1974) have recently reviewed these criteria and discussed their own methods for practical use of same. I here summarize my use of these criteria in order of their overall usefulness.

1. Ex-group comparisons. For a given character, a survey was made of the distribution of its states among members of closely and successively more distantly related groups. If a state represented among members of one or more Nebria species is also represented among members of other groups, that state was judged (in the absence of contradictory evidence) to be plesiotypic. The assumption made was that widespread occurrence results from common ancestry and not from

independent acquisition (i.e. convergence). For example, members of some Nearctic Nebria species and those of all related genera lack frontal pale spots. Therefore, presence of these spots is probably apotypic, their absence plesiotypic.

The character chosen for the above example is a two-state character; and, as such, polarity of its transformation series is determined simply by recognition of either the plesiotypic or the apotypic state. Many characters, however, are represented by many states--i.e. are multi-state characters--and determination of the pleisiotypic state is not of itself sufficient for determination of polarity and sequence of the entire transformation series. In analysing multi-state characters, an attempt was made to interpret states as elements of a "graded series" (Ball, 1975; the "morphocline" concept of Maslin, 1952), from most pleisiotypic (determined just as for two-state characters) to most apotypic (often recognized as the opposite extreme among states). Judgments on the relative apotypy of different intermediate states were aided by reference to ex-group comparisons and other criteria discussed below.

The evolution of some multi-state characters appears to have been extremely complex. Some transformation series exhibit multiple branches (and even secondary branching), reversal, and convergence, as interpreted through correlation with other transformation series (see below). For example, hypothetical reconstruction of the transformation series for shape of the preapical-shaft of the male median lobe (lateral aspect) is illustrated in Fig. 368 (character no. 116). The transformation is multiply-branched, and includes reversal steps (e.g from state

$116A^1$ to state 116B, reversing the step from state 116^1 to state $116A^1$). Most workers tend not to consider these complex transformations in their cladistic analyses. However, I have chosen to use these also because (1) they form a significant percentage of the total number of characters studied; (2) they do in fact contribute to the anaylsis of relationships among taxa; and (3) they provide an appropriate picture of the complexity of evolutionary change--a picture which is normally obscured when only simple characters (usually a minority) are analysed.

Results of ex-group comparisons provide, in general, the most useful criterion for determination of polarity in transformation series. This procedure requires two conditions, however, namely: (1) some previous (or at least independent) indication of relationships with and among other groups; and (2) representative material (specimens and other data) for comparative study. Fortunately, I have had access to abundant and diverse comparative material (see Appendix C for a list of taxa represented in samples studied), both at the University of Alberta and the California Academy of Sciences. Phylogenetic relationships among nebriine genera as well as those between tribe Nebriini and related "tribes" (i.e. Notiophilini and Opisthiini) had not been analysed previously. I therefore attempted to explore these relationships and thereby provide a tentative systematization of nebriine genera and their close relatives. This systematization was to serve as the framework for evaluation of data from ex-group comparisons. To this end, I expanded my comparative study to include representatives of most groups thought to be direct descendants of the primitive caraboid stock (see Appendix C),

including "hydradephagan" groups. Part of the systematization of these groups which resulted from cladistic analysis is presented in Fig. 369; and it was used as the basis for ex-group comparisons in this study. I reserve discussion of intergeneric and more inclusive relationships for a subsequent paper dealing expressly with this topic. I note here only that hypothetical relationships inferred represent a choice among different but almost equally plausible (and "parsimonious" (see below)) sets of relationships (see also comments on relationships of the *virescens* lineage, section 4.13).

2. *Character correlations*. According to Ekis (1977) and Hennig (1966), transformation series the polarity of which have been determined with some degree of confidence, can be used to infer polarity in transformations of other characters in which evolutionary sequence is less easily inferred. I found this criterion very useful, especially in working with complex, multi-state characters. However, its use requires further explanation than that provided by the above authors because, in and of themselves, transformations of different characters (except perhaps two or more characters of a single, integrated, adaptive complex) are not necessarily correlated. It is only through reference to a set of tentative hypotheses of relationship (as suggested by analyses of distributions of character states in transformations with established polarity) that polarity in other series can be inferred. For example, if members of species *A* and *B* share apotypic states of one or more characters for which transformation polarities are confidently established, a tentative hypothesis of relationship with species *C* (members of which exhibit the plesiotypic state(s) of this(these) character(s)) is as

illustrated in Fig. 370A. If the distributions of states of another character is such that A and C (but not B) share a given state, and we accept the hypothetical relationships noted above, then it follows that either (1) the shared state is plesiotypic and the apotypic state is restricted to members of species B (Fig. 370C), or (2) the shared state is apotypic and its occurrence in A and C is due to convergence (Fig. 370B). In the absence of other evidence or criteria, acceptance of the least complex (most "parsimonious"; see Platnick, 1975) explanation (i.e. (1) above) is preferred. The third option here is to reject the original hypotheses of relationship, based on evidence from this new character.

3. Group trends. Ball (1975) noted that within groups, certain characters "appear to follow the same evolutionary development [transformation] in many independent lineages". Members of *Nebria* species, for example, which inhabit highest montane habitats tend (without regard to their phylogenetic relationships) to have hindwings reduced, elytra shortened and with reduced humeral angles, metasterna shortened, and appendages lengthened. Members of species inhabiting extreme lowland habitats, especially in relatively arid areas, tend to have pale appendages and, in some instances, pale bodies. In general, repeated, independent transformations of characters in which such group trends appear were correlated with one another; and their respective polarities were thereby determined simultaneously.

4. Correlation with adaptive significance. Character states (of structural and other characters) evidently correlated with specialized (presumably apotypic) behavior could themselves, on this basis, be

interpreted as apotypic. For example, unique structural characteristics of the tarsi of N. ingens adults can be correlated with their observed ability to walk over exposed stone surfaces underwater. This behavior and its structural correlates were both judged to be apotypic. Such clear relationships between structure and function were infrequently recognized among Nearctic Nebria; and this criterion was, therefore, used in few instances only. Mouthparts and genitalia collectively form functional/adaptive complexes, characters of which are numerous and, presumably, not fully independent of each other. It should therefore be possible to determine polarity of transformations in several of these characters simultaneously if one or only a few can be correlated with apotypic function (e.g. feeding or mating behavior).

5. In-group comparisons. In some instances, the evolution of characters (and resultant diversity of character states) among members of a single group is so great that ex-group comparisons and other criteria are of little or no use in determination of sequence and/or polarity in transformations. In analyses of such characters, I resorted to so-called "in-group" comparisons (Ball, 1975; Ross, 1974). Procedure was as follows: (1) determine the character state exhibited by members of species judged to be (on other grounds) the most plesiotypic ("primitive"); (2) accept this character state as plesiotypic; and (3) determine transformation sequence for the other states by correlation with other transformations (see above). This criterion is, admittedly, weak and fraught with opportunities for misinterpretation. Nonetheless, used as a last resort, and then only with due caution, it can help resolve some questions. For example,

transformation series of several characters of the male median lobe were determined using this criterion. A major difficulty was encountered, however. In males of N virescens, the species judged to be most "primitive", the median lobe exhibits several character states judged to be apotypic (based on ex-group comparisons). I then considered as plesiotypic states represented in members of the species judged to be next most "primitive", namely members of the gyllenhali lineage; and transformation series which correlated well with other series were obtained. The major problem with this criterion is evident from the above, namely, that members of taxa judged to be"primitive" based on some or even most characters, may be expected to exhibit both plesiotypic and apotypic states for different characters (including the character of interest).

I did not find Hennig's (1966) criterion of "chorological progression" useful in analysis of characters for Nebria species and, therefore, will not consider it here.

The transformations of some characters studied could not be determined using any of the above criteria. In such instances, distributions of character states among Nearctic taxa were either without apparent pattern or otherwise too complex to interpret. These characters could not be used in the cladistic analysis of taxa. Analysis of many other characters required use of several criteria, in combinations, in order to recognize transformation patterns.

Procedure for cladistic analysis.--After transformation series of characters had been determined, distributions of their apotypic states among members of Nearctic species were studied. I consider the

biological species (Mayr, 1969) to be the basic phylogenetic unit [the term 'phylogenetic relationship', by definition, cannot be applied logically to infraspecific entities]. Consequently, a single state for each character was chosen to represent members of all populations (including those of different subspecies). Except when evidently inappropriate, the state of choice was, in each instance, the most plesiotypic state represented among species members. The effect, if any, of this choice was to reduce the number of synapotypies recognized for any two species, specifically by eliminating those synapotypies which are not universal among members of both species. I suggest that, consequently, the significance of those synapotypies finally recognized was increased.

The next step was recognition of species pairs (sister species) based on the criterion of synapotypy. By applying this criterion repeatedly, successively more inclusive groups were recognized. Unfortunately, this procedure was greatly complicated by a high level of discordance (incongruence) in patterns of synapotypy for different characters among species and groups. In such instances, I resorted to three additional steps in an attempt to reduce discordance (or at least recognize and evaluate its source). First I reassessed judgments on polarities of particular transformation series involved in discordant patterns. In some instances, I was able to resequence series or reverse their polarities through correlations with other transformations (criterion "2" above) as suggested by new tentative hypotheses on relationship. Residual discordance was then examined by plotting the distributions of character states of all characters studied on different cladograms, each reflecting a specific set of

relationships suggested by one of the discordant patterns of synapotypy. For each cladogram, I calculated the total number of 'extra evolutionary steps' (i.e. instances of convergence and reversal) required to account for the distributions of character states for all characters over the set of relationships proposed. Cladograms were then compared directly. Based on the assumption that divergence is more common than convergence or reversal in the evolution of characters, and on the contention that least complex explanations for observed phenomena are to be preferred in general, cladograms requiring the fewest extra evolutionary steps were selected as preferred hypotheses of phylogenetic relationship.

In few instances (for example, in reconstruction of relationships among members of the _ovipennis_ species group), two or more cladograms were found to be almost equally parsimonious. At this point, I again focused attention on the discordant characters and reinterpreted these according to the character weighting scheme proposed by Hecht (1976) and Hecht and Edwards (1977). By ignoring discordance in "low weight" characters and giving emphasis to that in "high weight" characters (i.e. those referable to Hecht's weighting groups "IV" and "V"), I was able to evaluate the relative significance of discordance in each cladogram and, ultimately, choose the one with least significant discordance.

4.12 Cladistic analysis

A total of 318 structural and natural history characters were analysed (through procedures outlined above), 171 of which were then used in a cladistic analysis of Nearctic species and their relatives.

Remaining characters include (1) those in which transformations could not be interpreted (see above), (2) those that are represented among Nebria members by single states judged to be plesiotypic (i.e. symplesiotypic for genus Nebria), and (3) those that are represented by single apotypic states in members of single species (i.e. autapotypic). As noted in section 3.33, all Palaearctic taxa presumed to be closely related to Nearctic taxa were also analyzed. Results of studies to determine transformation series of characters are presented in Tables 14 and 15. The former lists character states judged to be symplesiotypic among all Nebria members. The latter lists all other characters and presents for each the sequence and relative apotypy of character states and the criterion(-a) used for determination of polarity and sequence.

The distributions of character states among Nearctic Nebria and their Palaearctic relatives are summarized and illustrated in Fig. 372. Refer to the figure legend for an explanation of notation, symbols, and format used (modified from Griffiths, 1972).

Table 14. Character states plesiotypic[1] for Nearctic Nebria species.

Character	Character state
Supraorbital setae	one pair (posterior pair)
Vertex macrosculpture	smooth
Occiput shape	evenly broad, not abruptly constricted (i.e. "necked")
Setae on antennal scape	one
Setae on clypeus	one pair (mediolaterally)
Setae on labrum	three pair, across apical margin
Apex right mandible	not hooked
Mandibular scrobe	well-developed
Setae in mandibular scrobe	one present
Form maxilla	ventrolaterally flat, without spiniform processes
Form ligula	longitudinally carinate in midline
Setae on ligula	one pair (apicomedially)
Labial palpus	penultimate and terminal palpomeres approximately equal in length
Mentum M_1 setae	one pair, at base of mentum tooth
Mentum M_4 setae	absent
Form gula	without spiniform processes or ridge
Base of pronotum	without margination
Setae on prosternal intercoxal process	none

Table 14. (continued)

Closure anterior coxal cavity	open posteriorly
Perforation anterior coxal cavity	uniperforate
Separation anterior coxal cavities	confluent
Elytral vestiture	without pubescence
Elytral internal plica	simple, keel-like, extended to but not across epipleuron
Scutellar striole	short, medial to first complete stria, not joined with same basally
No. of complete striae	eight
Macrosculpture elytral intervals	smooth (excluding catenations)
Hindwing: marginal cell between $P+Cu_2$ and E_1 veins	without sclerotized microtrichial field
Metepimeron	apparently absent
Closure middle coxal cavity	disjunct
Separation middle coxal cavities	confluent
Closure hind coxal cavity	conjunct
Separation hind coxal cavities	confluent
Setae on front coxa	none

Table 14. (continued)

Setae on front trochanter	one (ventroapically)
Setae on middle trochanter	one (ventroapically)
Setae on hind trochanter	none
Front tibial antenna cleaner	simple, sulcate
Front tibial spurs	obliquely isochaetous
Male hind tarsomeres	without ventral pads of setae
Abdominal sterna	dorsolaterally carinate, but not otherwise modified for elytra lock function
Basal piece (male genitalia)	fused with base of median lobe
Internal sac median lobe	present, eversible
Setae on parameres	both asetose
Form eighth sternum	split medially, in form of two hemisterna
Vestiture eighth sternum	without pubsecence
Setae on middle one-third of apical margin each eighth hemisternum	none
Setae on lateral one-third of apical margin each eighth hemisternum	none
Setae on medial margin of each hemisternum	none
Length apodeme each eighth hemisternum	medium

Table 14. (continued)

Reinforcement rod on each eighth hemisternum	absent
Proctiger integrity	moderately sclerotized
Vestiture of proctiger	glabrous, asetose
Paraprocts integrity	moderately sclerotized
Vestiture of paraprocts	glabrous, asetose
Position apodeme of valvifer	dorsal on basal margin
Form coxostylus	unilobate, unsegmented, without attached "teeth"
Vestiture coxite region (ventral surface)	asetose, glabrous
Symmetry vestibular chamber bursa copulatrix	symmetrical
Separate dorsal or ventral bursal chambers	none
Spermathecal gland form	none
Reinforcement rod in oviduct	present

[1] Character states which are judged to be synapotypic for Nebria members and those of other related taxa are considered (relatively) symplesiotypic for Nebria alone and are, therefore, listed here.

Table 15. Phylogenetic classification of states of characters used in cladistic analysis of Nearctic *Nebria* species.

No.	Character	Character state[1] Plesiotypic (open squares)	Apotypic (solid squares)[2]	Criterion[3]
	Habitus:			
1	Overall size	small	very small=1^1	a,b,c
			medium=1^2	
			large=$1A^1$ (1^2)	
			very large=$1B^1$ ($1A^1$)	
			small=$1A^2$ (1^2)	
			very small=$1B^2$ ($1A^2$)	
			medium=$1B^3$ ($1A^2$)	
2	Relative size, by sex	medium	males larger than females=2	a
3	Relative head size	medium	slightly large=3	a,e

Table 15. (continued)

			moderately large=3A (3)	
			markedly large=3B (3A)	
4	Relative head size	equal in males	larger in females=4^1	a,e
			larger in males=4^2	
5	Relative head width	medium	slightly wide=5	a,e
			markedly wide=5A (5)	
			extremely wide=5B (5A)	
6	Relative pronotum size	large	medium=6	a,b,e
			slightly large=$6A^1$ (6)	
			moderately large=$6B^1$ ($6A^1$)	
			markedly large=6C ($6B^1$)	
			small=$6B^3$ ($6A^1$)	
			slightly small=$6A^2$ (6)	
			small=$6B^2$ ($6A^2$)	
7	Relative pronotum width	moderately wide	medium=7	a,b,e
			slightly wide=$7A^1$ (7)	

Table 15. (continued)

			moderately wide=$7B^1$ ($7A^1$)	
			markedly wide=7C ($7B^1$)	
			extremely wide=7D (7C)	
			slightly narrow=$7B^3$ ($7A^1$)	
			slightly narrow=$7A^2$ (7)	
			moderately narrow=$7B^2$ ($7A^2$)	
8	Relative elytra length	short	medium=8	a,c,e
			slightly long=$8A^1$ (8)	
			markedly long=$8B^1$ ($8A^1$)	
			slightly short=$8A^2$ (8)	
			moderately short=$8B^2$ ($8A^2$)	
			markedly short=8C ($8B^2$)	
9	Relative elytra length, by sex	distinctly longer in females	not or slightly longer in females=9	a,e
10	Relative elytra width	medium	slightly wide=10^1	b,e
			moderately wide=$10A^1$ (10^1)	

Table 15. (continued)

			markedly wide=10B ($10A^1$)	
			medium=10C (10B)	
			slightly narrow=$10A^3$ (10^1)	
			slightly narrow=10^2	
			moderately narrow=$10A^2$ (10^2)	
	Color:			
11	Head color	piceous or black	brown=11	a,b,e
			rufous=11A (11)	
			orange-tan or yellow=11B (11A)	
12	Frontal pale spots	absent	present=12	a,b
13	Pronotum color	piceous or black	brown=13	a,c,e
			rufous=13A (13)	
			orange-tan or yellow=13B (13A)	
14	Elytra color	piceous or black	brown=14	a,c,e
			orange-tan=14A (14)	
			yellow=14B (14A)	

Table 15. (continued)

15	Leg color	piceous or black	brown=15	a,c,e
			rufous=15A (15)	
			orange-tan or yellow=15B (15A)	
	Reflection:			
16	Metallic reflection on head	faint	moderate=16^1	a,b,e
			distinct=$16A^1$ (16^1)	
			absent=16^2	
			faint=$16A^2$ (16^2)	
			moderate=16B ($16A^2$)	
17	Metallic reflection on pronotum	faint	moderate=17^1	a,b,e
			distinct=$17A^1$ (17^1)	
			faint=$17A^3$ (17^1)	
			absent=$17B^1$ ($17A^3$)	
			absent=17^2	
			faint=$17A^2$ (17^2)	
			moderate=$17B^2$ ($17A^2$)	

Table 15. (continued)

18	Metallic reflection elytra	faint	moderate=18^1 distinct=$18A^1$ (18^1) faint=$18B^1$ ($18A^1$) absent=18C ($18B^1$) absent=18^2 faint=$18A^2$ (18^1) moderate=$18B^2$ ($18A^2$)	a,b,e
19	Metallic reflection on thoracic venter	absent	faint=19 moderate=$19A^1$ (19) absent=$19A^2$ (19)	a,e
20	Metallic reflection on abdominal venter	absent	faint=20 moderate=20A (20)	a,e
	Luster:			
21	Head luster	moderately dull	faintly shiny=21 markedly shiny=21A (21)	b,c,e

Table 15. (continued)

			very shiny=21B (21A)	
22	Pronotum luster	moderately dull	faintly shiny=22^1	b,c,e
			markedly shiny=22A (22^1)	
			very shiny=22B (22A)	
			very dull=22^2	
23	Elytra luster	moderately dull	faintly shiny=23^1	b,c,e
			markedly shiny=23A (23^1)	
			very shiny=23B (23A)	
			very dull=23^2	
	Microsculpture:			
24	Frons	moderate	faint=24	a,b,c,e
	microsculpture:		more or less effaced=24A (24)	
	impression			

Table 15. (continued)

25	Pronotum microsculpture: impression	deep	moderate=25^1	a,b,c,e
			faint=$25A^1$ (25^1)	
			more or less effaced=25B ($25A^1$)	
			absent=25C (25B)	
			very deep=$25A^2$ (25^1)	
			very deep=25^2	
26	Pronotum microsculpture: alveolar shape	isodiametric	slightly transverse=26^1	a,b,c,e
			absent=26^2	
27	Elytra microsculpture: impression	deep	moderate=27	a,b,c,e
			faint=$27A^1$ (27)	
			deep=$27A^2$ (27)	
			very deep=27B ($27A^2$)	
28	Elytra microsculpture: alveolar shape	isodiametric	irregular (mixed shapes, mainly isodiametric and slightly transverse)=28	a,b,c,e
			slightly transverse=28A (28)	

Table 15. (continued)

			moderately transverse=28B (28A)	
			markedly transverse=28C (28B)	
			stretched lines with no or few meshes=28D (28C)	
	Head:			
29	Shape of genae	not inflated	slightly inflated=29	a,e
			moderately inflated=29A (29)	
			markedly inflated=29B (29A)	
30	Shape of genae, by sex	same in both sexes	more inflated in males=30[1]	a,e
			more inflated in females=30[2]	
31	Shape of occiput	not inflated	slightly inflated=31	a,e
			moderately inflated=31A (31)	
			markedly inflated=31B (31A)	
32	Shape of occiput, by sex	same in both sexes	more inflated in males=32[1]	a,e
			more inflated in females=32[2]	
33	Eye size	moderate	slightly reduced=33	a
			moderately reduced=33A (33)	

Table 15. (continued)

34	Eye shape	moderately convex	markedly convex=34^1	a
			slightly flat=34^2	
			moderately flat=34A (34^2)	
35	Relative length antenna	medium	moderately long=35	a,c,e
			markedly long=$35A^1$ (35)	
			extremely long=$35B^1$ ($35A^1$)	
			slightly long=$35B^2$ ($35A^1$)	
			slightly long=$35A^2$ (35)	
			markedly long=$35B^3$ ($35A^2$)	
36	Pubescence of fourth antennomere	glabrous throughout	apical one-third sparsely pubescent=36	a,b
37	Relative length antennal scape	medium	slightly short=37^1	a,b,c,e
			markedly short=37A (37^1)	
			long=37^2	

Table 15. (continued)

38	Axis of antennal scape	straight	very slightly arcuate=38 moderately arcuate=38A (38) markedly arcuate=38B (38A) bisinuate=38C (38B)	a,b,e
39	Shape antennal scape	cylindrical	slightly narrowed basally=39^1 moderately narrowed basally=39A (39^1) markedly narrowed basally=39B (39A) convex anteriorly at middle=39^2	a,b,e
40	No. setae on pedicel	one	two or three=40 three only=40A (40)	a
41	Shape flagellar antennomeres	medium length and width	slightly elongate, more slender=41 markedly elongate, very slender=$41A^1$ (41) slightly elongate, moderately slender=$41B^1$ ($41A^1$) medium length and width=41C ($41B^1$) slightly short, slightly broad=41D (41C)	a,b,c,e

Table 15. (continued)

			medium length and width=$41A^2$ (41) slightly short, slightly broad=$41B^2$ ($41A^2$)	
42	Shape mandibles	moderately explanate basolaterally	broadly explanate basolaterally=42	a,e
43	Shape tooth of ligular margin	blunt and/or medium length	sharp, long=43^1 absent, margin truncate=43^2	a,e
44	Paraglossae	separate, lobate	separate, but minute, dentiform=44 adnate, completely fused with ligula=44A (44)	a
45	No. setae on penultimate labial palpomere	two	three=45 two=45A (45)	a,b
46	Shape tooth of mentum	moderately or deeply bifid	slightly emarginate medially=46 truncate apically=46A	a,e
47	Position of M_2 setae on mentum	moderately distant from basal margin	near basal margin=47^1 very remote from apical margin=47^2	a,e

Table 15. (continued)

48	M_3 setae on mentum	present	absent=48	a,e
49	Tooth of epilobe of mentum	moderate length	minute=49^1 long=49^2	a,e
	Pronotum:			
50	Overall shape	semiovoid	moderately cordate=50^1 markedly cordate=$50A^1$ (50^1) extremely cordate=$50B^1$ ($50A^1$) moderately cordate=$50B^2$ ($50A^1$) slightly cordate=$50A^2$ (50^1) slightly cordate=50^2	a,b,e
51	Overall convexity	markedly convex	moderately convex=51 markedly convex=51A (51)	a,e
52	Shape lateral margin	moderately arcuate	markedly arcuate=52^1 moderately arcuate=$52A^1$ (51^1) slightly arcuate=52^2	a,b,e

Table 15. (continued)

			slightly arcuate and faintly sinuate anteriorly $=52A^2$ (52^2)	
53	Depth basal sinuation of lateral margin	absent	faintly sinuate=53	a,b,e
			moderately sinuate=53A (53)	
			markedly sinuate=$53B^1$ (53A)	
			very deeply sinuate=53C ($53B^1$)	
			faintly sinuate=$53B^2$ (53A)	
			slightly sinuate=$53B^3$ (53A)	
54	Length basal sinuation of lateral margin	absent	short=54	a,e
			moderate=54A (54)	
			long=$54B^1$ (54A)	
			very long=$54C^1$ ($54B^1$)	
			short=$54B^2$ (54A)	
			moderate=$54C^2$ ($54B^2$)	
			slightly short=$54B^3$ (54A)	

Table 15. (continued)

55	Width lateral explanation	medium	broad=55^1	a,c,e
			moderate=55A (55^1)	
			narrow=55^2	
56	Relative width of base	medium	slightly narrow=56^1	a,b,e
			markedly narrow=$56A^1$ (56^1)	
			slightly broad=56^2	
			moderately broad=$56A^2$ (56^2)	
			very broad=56B ($56A^2$)	
57	Shape basal margin	truncate	slightly bisinuate=57^1	a,b,e
			markedly bisinuate=$57A^1$ (57^1)	
			slightly sinuate laterally=$57A^2$ (57^1)	
			slightly bisinuate and convex medially=57^2	
			slightly sinuate laterally=57^3	
			markedly sinuate laterally=$57A^3$ (57^3)	
			convex medially=57^4	

Table 15. (continued)

58	Length (projection) of apical angles	medium	moderately long=58^1 very long, projected=58A (58^1) moderately short=58^2	b,e
59	Width of apical angles	medium	slightly broad=59^1 very broad=$59A^1$ (59^1) medium=$59A^3$ (59^1) slightly narrow=59^2 markedly narrow=$59A^2$ (59^2)	b,e
60	Shape apex of apical angles	moderately rounded	pointed=60^1 broadly rounded=60^2 moderately rounded=60A (60^2)	a,e
61	Shape basal angles	rectangular	rectangular, projected posteriorly=61^1 obtuse=61^2 rectangular=61A (61^2) acute=61^3	a,b,c,e

Table 15. (continued)

62	Impression lateral margination	medium	slightly shallow=62 faint=62A (62) very faint=62B (62A)	a,b,e
63	Width lateral margination	medium	slightly wide=63^1 slightly narrow=63^2 markedly narrow=63A (63^2)	b,e
64	Posterior transverse impression	deep, narrow	slightly shallow=64^1 moderately shallow=64A (64^1) very deep, narrow=64^2 deep, but broad=64^3	b,e
65	Depth basal foveae	deep	slightly shallow=65 moderately shallow=65A (65) markedly shallow=65B (65A)	a,b,e
66	Width basal foveae	extremely broad	markedly broad=66 moderately broad=66A (66) slightly broad=$66B^1$ (66A)	a,b,e

Table 15. (continued)

			medium=66C ($66B^1$)	
			slightly narrow=$66D^1$ (66C)	
			moderately narrow=$66E^1$ ($66D^1$)	
			markedly narrow=66F ($66E^1$)	
			extremely narrow=66G (66f)	
			moderately broad=$66D^2$ (66C)	
			markedly broad=$66E^2$ ($66D^2$)	
			markedly broad=$66B^2$ (66A)	
67	Orientation of basal foveae	parallel	slightly divergent basally=67	a,b,e
			moderately divergent basally=67A (67)	
			markedly divergent basally=67B (67A)	
68	Midlateral seta	present	absent=68	a
69	Tubercle medial to midlateral seta	absent	present=69	a,e
70	Basolateral seta	present	absent=70	a

Table 15. (continued)

	Prosternum:			
71	Intercoxal process	sublanceolate	moderately lanceolate=71^1	a,b,e
			markedly lanceolate=$71A^1$ (71^1)	
			lanceolate, narrow=$71A^2$ (71^1)	
			sublanceolate=$71A^3$ (71^1)	
			spatulate=71^2	
72	Macrosculpture intercoxal process	smooth	rugose=72	a,e
73	Margination intercoxal process	complete	complete, except at apex=73	a,e
			present laterally in basal half only=$73A^1$ (73)	
			present only anteromedial to coxa=$73B^1$ ($73A^1$)	
			present laterally in basal half, but interrupted at base=$73B^2$ ($73A^1$)	
			complete (or nearly so across apex)=$73A^2$ (73)	

Table 15. (continued)

	Elytra:			
74	Overall silhouette	rectangular	subrectangular=74	a,c
			subovoid=$74A^1$ (74)	
			ovoid=74B ($74A^1$)	
			subovoid, but sides straight in basal half= $74A^2$ (74)	
75	Overall convexity	medium	slightly flattened=75^1	a,b,e
			moderately flattened=$75A^1$ (75^1)	
			very convex=$75A^3$ (75^1)	
			markedly convex=75^2	
			very convex=$75A^2$ (75^2)	
76	Length basal margination	very long	moderately long=76	a,b,c,e
			slightly long=76A (76)	
			medium=76B (76A)	

Table 15. (continued)

			slightly short=76C (76B)	
			moderately short=76D (76C)	
			markedly short=76E (76D)	
			extremely short=76F (76E)	
77	Shape humerus	rectangular	distinctly angulate, but slightly rounded=77	a,c
			moderately rounded=77A (77)	
			markedly rounded=77B (77A)	
			extremely rounded=77C (77B)	
			slightly flattened=77D (77C)	
			obliterated=77E (77D)	
78	Humeral carina	absent	faint, vaguely linear=78^1	a,c,e,
			distinct, moderately sharp, not projected =$78A^1$ (78^1)	
			distinct, sharp, slightly projected=78B ($78A^1$)	

Table 15. (continued)

			markedly sharp, moderately projected=78C ($78B^1$)	
			extremely sharp, markedly projected=78D (78C)	
			present as minute marginal tooth=78^2	
			present as distinct marginal tooth=$78A^2$ (78^2)	
79	Subhumeral sinuation	very faint, very shallow	distinct but shallow=79^1	a,e
			moderately deep=$79A^1$ (79^1)	
			markedly deep=79B ($79A^1$)	
			absent=79^2	
			faint, shallow, slightly displaced anteriorly= 79^3	
			distinct, shallow, displaced anteriorly=$79A^2$ (79^3)	
80	Shape apex	bluntly pointed, at midline, sutural margin straight	rounded, slightly lateral from midline; sutural margin straight=80	a,b,e
			broadly pointed, displaced laterally; sutural margin arcuate to apex=$80A^1$ (80)	

Table 15. (continued)

			narrowly pointed, displaced laterally; sutural margin sinuate=80B ($80A^1$)	
			narrow, obliquely truncate, displaced laterally; sutural margin straight=$80A^2$ (80)	
			broad, rounded, but apically truncate, slightly displaced laterally; sutural margin straight= $80A^3$ (80)	
81	Depth of striae	medium	moderately shallow=81^1	a,b,c,e
			markedly shallow=$81A^1$ (81^1)	
			moderately deep=81^2	
			markedly deep=$81A^2$ (81^2)	
			extremely deep=81B ($81A^2$)	
			medium=$81A^4$ (81^2)	
			medial striae medium, lateral striae very shallow =81^3	

Table 15. (continued)

			medial striae slightly shallow, lateral striae almost obliterated=81A^3 (81^3)	
82	Convexity of intervals	moderately flat	very faintly convex=82	a,b,e
			slightly convex=82A (82)	
			moderately convex=82B (82A)	
			markedly convex=82C^1 (82B)	
			extremely convex=82D (82C^1)	
			slightly convex=82C^2 (82B)	
83	Continuity of intervals	uniform, uninterrupted	faintly catenate=83	a,b,e
			moderately catenate=83A (83)	
			markedly catenate, but not tuberculate=83B^1 (83A)	
			markedly catenate, tuberculate=83C^1 (83B^1)	
			moderately catenate=83C^2 (83B^1)	
			faintly catenate=83B^2 (83A)	

Table 15. (continued)

84	Pores for discal setae	slightly foveate	moderately foveate=84^1	a,b,e
			broadly foveate=84A (84^1)	
			deeply and broadly foveate=84B (84A)	
			weakly foveate=84C (84B)	
			minute, barely evident=84^2	
85	Basal pore	present	absent=85	a,e
86	Setae on fifth interval	none	few=86	a,b,e
			none=$86A^1$ (86)	
			many=$86A^2$ (86)	
			few or none=86B ($86A^2$)	
87	Setae on seventh interval	none	few=87	a,b,e
			many=$87A^1$ (87)	
			few or none=87B ($87A^1$)	
			none=$87A^2$ (87)	

Table 15. (continued)

Wings:				
88	Size	full-sized	truncate at stigma, broad=88^1	a,c
			truncate and narrow=$88A^1$ (88^1)	
			short and narrow, stigma barely evident=$88B^1$ ($88A^1$)	
			short, lobate, some venation present=88C ($88B^1$)	
			strap-like, very thin, elongate=88D (88C)	
			scale-like, short=88E (88D)	
			full-length, but narrowed=88^2	
			slightly short, narrowed=$88A^2$ (88^2)	
89	Shape oblongum cell	almost quadrate, stalk minute	slightly narrowed posteriorly, stalk short=89^1	a,b,e
			slightly narrowed posteriorly, stalk long=$89A^1$ (89^1)	
			faintly triangular, markedly narrowed, stalk medium=$89A^2$ (89^1)	

Table 15. (continued)

			distinctly triangular, stalk long=89B ($89A^2$)	
			broad, rounded posteriorly, stalk minute=89^2	
	Pterothoracic venter:			
90	Mesosternum macrosculpture	moderately punctate	sparsely, faintly punctate=90	a,e
			smooth, impunctate=90A (90)	
			sparsely, faintly punctate=90B (90A)	
91	Mesepisternum macrosculpture	moderately punctate	sparsely, faintly punctate=91	a,e
			faintly punctulate=91A (91)	
			smooth, impunctate=91B (91A)	
92	Metasternum macrosculpture	moderately punctate	sparsely, faintly punctate=92	a,e
			faintly punctulate=92A (92)	
			smooth, impunctate=92B (92A)	
93	Metepisternum macrosculpture	punctate	faintly punctulate=93	a,e
			smooth, impunctate=93A (93)	

Table 15. (continued)

94	Relative length metasternum	moderately long	very slightly short=94^1	a,e
			slightly short=94A (94^1)	
			moderately short=94B (94A)	
			markedly short=94C (94B)	
			very short=94D (94C)	
			extremely short=94E (94D)	
			very long=94^2	
95	Margination metasternum anterior intercoxal process	complete, deep throughout	complete, moderate throughout=95	a,b,e
			complete, faint at middle=95A (95)	
			incomplete, only vague depression medially=95B (95A)	
			incomplete, absent medially=95C (95B)	
	Legs:			
96	Relative leg length	medium	slightly long=96^1	a,b,e
			moderately long=$96A^1$ (96^1)	
			markedly long=96B ($96A^1$)	

Table 15. (continued)

			extremely long=$96C^1$ (96B)	
			slightly long=$96C^2$ (96B)	
			slightly short=96^2	
			moderately short=$96A^2$ (96^2)	
			slightly long=$96A^3$ (96^2)	
97	No. setae at base of hind coxa	one	few=97	a,b,e
			many=97A (97)	
			few=97B (97A)	
			one=97C (97B)	
98	Dorsal groove on middle tibia	distinct, present except at apex	distinct even near apex=98^1	a,b,e
			distinct only on middle one-third=98^2	
			absent; dorsum flat or convex=98B (98^2)	
99	Brush of setae on dorsum middle tibia	moderately dense	sparse=99	a,e

Table 15. (continued)

100	Ventral pads of setae on mesothoracic tarsomeres	present	absent=100	a
101	Shape ventroapical margin fourth tarsomere hind tarsus	truncate	slightly lobate laterally=101 moderately lobate laterally=$101A^1$ (101) markedly lobate laterally=$101B^1$ ($101A^1$) extremely lobate laterally=101C (101B) slightly lobate laterally=$101A^2$ (101) faintly lobate laterally=$101B^2$ ($101A^2$)	a,b,e
102	Dorsal pubescence tarsomeres	present	absent=102 present=102A (102)	a,e
	Abdomen:			
103	Setae on second visible sternum	none	patch of setae medially=103^1 none=$103A^1$ (103^1) one pair of paramedial setae present=103^2	a,b,e

Table 15. (continued)

			patch of setae medially=$103A^2$ (103^2)	
104	No. posterior paramedial setae on third to fifth visible sterna	one pair	few pairs=104 many pairs=$104A^1$ (104) few pairs=104B ($104A^1$) one pair=$104A^2$ (104)	a,b,e
105	No. anterior paralateral setae on third to fifth visible sterna	none	few pairs=105 many pairs=$105A^1$ (105) few pairs=105B ($105A^1$) none=$105A^2$ (105)	a,b,e
106	No. paramedial setae male sixth visible sternum	one pair	two or more pairs=106	a,b,e
107	No. paramedial setae female sixth visible sternum	two or more pairs	one pair=107	a,b,e

Table 15. (continued)

108	Macrosculpture first visible sternum	moderately punctate	faintly, sparsely punctate=108^1 faintly punctulate=108A (108^1) smooth, impunctate=108B (108A) coarsely, densely punctate=108^2	a,e
	Male genitalia:			
	Median lobe:			
109	Shape basal bulb	quadrate, broadly open basally	rounded, partially closed basally=109	a,b
110	Dorsobasal piece	present as collar on basal bulb	present as dorsal midline crest=110	a,b
111	Thickness mid-shaft	medium	thick=111^1 very thick=111A (111^1) slender=111^2	a,b,e
112	Taper mid-shaft	moderately narrowed apically	cylindrical, diameter roughly equal throughout= 112^1 moderately narrowed basally=112A (112^1)	a,b,e

Table 15. (continued)

			markedly narrowed basally=112B (112A)	
			markedly narrowed apically=112^2	
113	Bend in axis of mid-shaft	less than 90°	90° or more, but less than 135°=113	a,b,e
			135° or more=$113A^1$ (113)	
			less than 90°=$113A^2$ (113)	
114	Cross-section shape mid-shaft	slightly compressed	moderately compressed=114^1	a,b,e
			markedly compressed=114A (114^1)	
			circular=114^2	
115	Right dorsal face mid-shaft	unmodified	faint indentation=115^1	a,b
			moderately deep pouch, directed basally=115A (115^1)	
			very deep pouch=115B (115A)	
			longitudinal groove lateral to dorsal ridge=115^2	
116	Shape preapical-shaft (lateral aspect)	narrow, margins almost parallel	moderately broad, moderately tapered apically= 116^1	a,b,e
			markedly broad, sharply tapered apically=$116A^1$ (116^1)	

Table 15. (continued)

			moderately broad, moderately tapered apically= 116B ($116A^{1}$)	
			extremely broad, truncate apically=116^{2}	
			very broad, subtruncate apically=$116A^{2}$ (116^{2})	
			very narrow, margins almost parallel=116^{3}	
			narrow, narrowest at base of apex=116^{4}	
117	Symmetry preapical-shaft (apical aspect)	symmetrical	asymmetrical, apical orifice deflected slightly right=117	a,b,e
			asymmetrical, orifice moderately deflected right= 117A (117)	
			asymmetrical, orifice markedly deflected right= 117B (117A)	
			asymmetrical, orifice extremely deflected right= 117C (117B)	
118	Symmetry preapical-shaft (dorsal aspect)	symmetrical	faintly deflected right=118	a,b,e
			slightly deflected right=118A (118)	

Table 15. (continued)

			moderately deflected right=$118B^1$ (118A)	
			markedly deflected right=$118C^1$ ($118B^1$)	
			symmetrical=$118B^2$ (118A)	
			slightly deflected right=$118C^2$ ($118B^2$)	
119	Shape preapical-shaft (dorsal aspect)	broadly tapered apically	narrowly tapered apically=119^1	a,b,e
			faintly tapered apically=119^2	
			slightly tapered basally=119A (119^2)	
120	Shape ventral margin preapical-shaft (lateral aspect)	straight or smoothly concave	faintly recurved subapically=120^1	a,b,e
			moderately recurved=120A (120^1)	
			markedly recurved=120B (120A)	
			abruptly deflected ventrally=120^2	
			slightly recurved apically=120^3	
121	Shape apex (ventral aspect)	broadly pointed	bluntly pointed=121^1	a,b,e
			shovel-shaped=$121A^1$ (121^1)	
			shovel-shaped, with minute lobe near middle= $121B^1$ ($121A^1$)	

Table 15. (continued)

			shovel-shaped, with moderate lobe near middle=121C ($121B^1$)	
			broadly pointed=$121A^2$ (121^1)	
			narrowly pointed=$121B^2$ ($121A^2$)	
			narrowly pointed=121^2	
122	Symmetry apex (ventral aspect)	symmetrical (centered on shaft)	asymmetrical, slightly deflected right=122	a,b,e
			asymmetrical, moderately deflected right=$122A^1$ (122)	
			asymmetrical, markedly deflected right=122B ($122A^1$)	
			asymmetrical, slightly or moderately deflected left=122C (122B)	
			symmetrical, centered on shaft=$122A^2$ (122)	
123	Plane of apex face (apical aspect)	vertical	horizontal=123^1	a,b,e
			twisted slightly left=123^2	
			markedly twisted left=$123A^1$ (123^2)	

Table 15. (continued)

			vertical=$123A^2$ (123^2)	
124	Length apex (lateral aspect)	medium	long=124^1	a,b,e
			short=124^2	
			very short=124A (124^2)	
125	Shape apex (lateral aspect)	bluntly pointed	blunt=125^1	a,b,e
			broadly blunt=$125A^1$ (125^1)	
			rounded=$125B^1$ ($125A^1$)	
			hooked=$125B^2$ ($125A^1$)	
			roundly hooked=125C ($125B^2$)	
			moderately pointed=125^2	
			narrow, sharply pointed=$125A^2$ (125^2)	
126	Axis of apex (lateral aspect)	straight	slightly deflected ventrally=126^1	a,b,e
			slightly recurved=126^2	
	Parameres:			
127	Symmetry parameres	asymmetric, right longer than left	symmetric, equal length=127^1	a,b,e
			asymmetric,right slightly longer than left=127^2	

Table 15. (continued)

128	Shape left paramere	broad, short	broad, slightly long, pointed apically=128^1 slightly narrow, slightly long=128^2 broad, moderately long=128^3	a,b,e
129	Shape right paramere	slender, long, arcuate	slender, very long=129^1 broad, moderately short=129^2	a,b,e
130	Right medial parameric sclerite	absent	present=130 absent=130A (130)	a,b,e
	Female genitalia:			
	Eighth sternum:			
131	Length setae on medial end apical margin	medium and long	medium only=131 long only=$131A^1$ (131) short only=$131A^2$ (131)	a,b,e
132	Density setae on medial end apical margin	medium	dense=132^1 sparse=132^2	a,b,e

Table 15. (continued)

133	Setae at middle of apical margin	present	absent=133	a
134	Width basal apodeme	medium	narrow=134	a,b,e
135	Shape basal apodeme	moderately emarginate, arms equal length	deeply emarginate, arms equal length=135 lateral arm slightly shortened=135A (135) lateral arm moderately shortened=135B (135A) lateral arm markedly shortened=135C (135B) lateral arm reduced to faint lobe=135D (135C) lateral arm obliterated=135E (135D)	a,b,e
	Proctiger:			
136	Shape	hemispheric, well sclerotized throughout	hemispheric, narrowly membranous apically=136 short, broad, extensive apical area membranous 136A (136)	a,b,e
	Paraprocts:			
137	Vestiture	sparsely pubescent	glabrous=137	a

Table 15. (continued)

138	Continuity with valvifer	very broadly continuous basally	broadly continuous basally=138	a,b.e
			moderately continuous basally=138A (138)	
			narrowly continuous basally=$138B^1$	
			broadly continuous basally=$138B^2$	
	Valvifers:			
139	Integrity	divided into lateral and medial areas, by intervening membranous area	medial area very lightly sclerotized=139	a,b,e
			medial area membranous=139A (139)	
140	Vestiture	setae on medial area and adjacent membrane	setae sparse, on medial sclerotized area only= 140	a,b,e
			asetose=140A (140)	
141	Length setae	short	absent=141^1	a,b,e
			medium only=141^2	

Table 15. (continued)

			medium and long=141A (141^2)	
142	Density setae	medium	sparse=142 absent=$142A^1$ (141) medium=$142A^2$ (141)	a,b,e
143	Shape basal apodeme	medium length, broad	short, very broad=143^1 medium length, slightly narrow=143^2	a,b,e
	Coxostylus:			
144	Vestige of tenth sternum	fused basally with base of coxostylus	separate, not fused basally with coxostylus=144	a,b,e
145	Fusion of coxite with stylus	fused medially and ventromedially	fused ventromedially but not medially=145	a,e
146	Shape stylus (ventral aspect)	slender, slightly arcuate, rounded apically	broad, moderately arcuate, pointed apically= 146^1 broad, slightly arcuate, spatulate apically= 146^2	a,b,e

Table 15. (continued)

147	Shape stylus (lateral aspect)	medium width, apex bluntly rounded, deflected dorsally	broad, apex narrowly rounded, straight=147^1 very broad, apex broadly rounded, straight=147^2	a,b,e
148	Length stylus	medium	slightly short=148^1 moderately short=148A (148^1) moderately long=148^2	a,b,e
149	Ventral diagonal row of setae (on coxite)	three to six medium length, setiform setae	one to four medium length, setiform setae=149^1 three to six medium length, spiniform setae=149^2 five or six long, spiniform setae=149A (149^2) two to four short, setiform setae=149^3	a,b,e
150	Mediodorsal row of setae (on stylus)	three to five medium length, setiform setae, row longitudinal	one to three medium length, setiform setae, row longitudinal=150^1 three to five medium length, spiniform setae, row diagonal=150^2	a,b,e

Table 15. (continued)

			two or three long, spiniform setae, row diagonal= 150A (150^2)	
			three or four medium length, setiform setae, row diagonal=150^3	
			three moderately long, setiform setae, row longitudinal=150^4	
151	Vestiture ventral surface	sparsely setose	asetose=151	a,b,e
152	Vestiture medial surface	densely setose subapically and and at middle	densely setose at middle only=152^1	a,b,e
			moderately setose subapically and at middle=152^2	
			densely to sparsely pubescent (very fine setae) subapically only=$152A^1$ (152^2)	
			glabrous=152B ($152A^1$)	
			sparsely setose subapically and at middle=$152A^2$ (152^2)	
			sparsely setose at middle only=$152A^3$ (152^2)	

Table 15. (continued)

	Bursa copulatrix:			
153	Longitudinal axis (lateral aspect)	simple, slightly deflected dorsally	faintly sigmoid=153	a,b,e
			moderately or markedly sigmoid=$153A^1$ (153)	
			sigmoid, but anterior end reduced=$153B^2$ ($153A^1$)	
			slightly deflected dorsally=$153A^2$ (153)	
			markedly deflected dorsally=$153A^3$ (153)	
			recurved posterodorsally=$153B^1$ ($153A^3$)	
154	Shape vestibular chamber (dorsal aspect)	gradually widened anteriorly	bell-shaped, simple=154	a,b,e
			bell-shaped, recurved posteriorly at sides= $154A^1$	
			bell-shaped, slightly constricted anteriorly= $154A^2$ (154)	
			bell-shaped, slightly constricted anteriorly, recurved posteriorly at sides=154B ($154A^2$)	

Table 15. (continued)

155	Shape spermathecal chamber (lateral aspect)	flat, thin	flat, thick=155 thinly fusiform=155A thick, apex moderately recurved dorsally=$155B^1$ (155A) thick, apex markedly recurved dorsally=155C ($155B^1$) thick, apex recurved ventrally=$155B^2$ (155A) thickly fusiform=$155B^3$ (155A) fusiform, markedly inflated basally=$155B^4$ (155A)	a,b,e
156	Length spermathecal chamber (lateral aspect)	slightly short	medium length=156^1 slightly long=$156A^1$ (156^1) markedly long=156B ($156A^1$) short=$156A^2$ (156^1) short=156^2 very short=$156A^3$ (156^2)	a,b,e

Table 15. (continued)

157	Shape spermathecal chamber (dorsal aspect)	broadly cordate, elongate	moderately broad, cordate=157^{1}	a,b,e
			broad, anteriorly truncate=157^{2}	
			subquadrate=$157A^{1}$ (157^{2})	
			trapezoidal, slightly narrowed anteriorly=157B ($157A^{1}$)	
			ovoid, slightly elongate=$157A^{2}$ (157^{2})	
			spatulate=157^{3}	
			broadly cordate=$157A^{3}$ (157^{3})	
			ovoid, slightly elongate=$157A^{4}$ (157^{3})	
			round=$157A^{5}$ (157^{3})	
			cordate, posterior margin emarginate=$157A^{6}$ (157^{3})	
158	Symmetry of spermathecal chamber (dorsal aspect)	symmetrical	slightly deflected left=158^{1}	a,b,e
			moderately deflected left=$158A^{1}$ (158^{1})	
			markedly deflected left=158B ($158A^{1}$)	
			slightly deflected right=$158A^{2}$ (158^{1})	

Table 15. (continued)

			moderately deflected right=158^2	
159	Accessory lobes on dorsum of spermathecal chamber	none	paired, elongate, thick, paramedial lobes, not associated with spermathecal duct insertion 159^1	a,b,e
			single, short, slender lobe in midline underlying spermathecal duct insertion=159^2	
			single, elongate, slender lobe in midline underlying spermathecal duct insertion=159A (159^2)	
			single, markedly elongate, slender lobe in midline underlying spermathecal duct insertion= 159B (159A)	
			none=159C (159B)	
			single, elongate, slender lobe in midline overlying spermathecal duct insertion=159^3	

Table 15. (continued)

160	Sclerite on dorsum of spermathecal chamber	none	small or large, flat plate anterior to spermathecal duct insertion (s.d.i.)=160^1	a,b,e
			medium-sized, flat plate, involuted medially, lateral margins recurved, anterior to s.d.i=$160A^1$ (160^1)	
			small, domed plate, not involuted medially, shape varied, anterior to or surrounding s.d.i.=$160B^1$ ($160A^1$)	
			oval plate, depressed medially, recurved laterally, anterior to s.d.i.=$160B^2$ ($160A^1$)	
			raised, horseshoe-shaped plate, depressed medially, s.d.i. centered in posterior half of plate=$160C^3$ ($160B^2$)	
			raised, horseshoe-shaped plate, depressed medially, s.d.i. centered in anterior half of plate=$160D^2$ ($160C^3$)	

Table 15. (continued)

small or large plate, shallowly or deeply invaginated medially (shape varied), anterior to s.d.i.=$160A^2$ (160^1)

large, quadrate, flat plate, surface crenulated, anterior to s.d.i.=$160A^3$ (160^1)

medium-sized oval plate, surface crenulated, anterior to s.d.i.=$160B^3$ ($160A^3$)

small oval plate, surface crenulated,at anterior end of chamber=$160C^1$ ($160B^3$)

very small plate, surface crenulated, at anterior end of chamber=$160D^1$ ($160C^1$)

small oval plate, faintly sclerotized, surface convoluted, at anterior end of chamber=$160C^2$ ($160B^3$)

elongate, slender, on dorsal accessory lobe=160^2

Table 15. (continued)

			small, quadrate plate, surface longitudinally convoluted, anterior to s.d.i.=160^3	
161	Sclerite in venter of spermathecal chamber	only an opaque reinforcement rod in midline, not sclerotized	opaque rod short, barely extended to chamber= 161^1	a,b,e
			opaque rod double-wide in midline=161^2	
			broad plate deeply infolded longitudinally in midline, s.d.i. between rod and plate=$161A^1$ (161^2)	
			as $161A^1$, but midline area everted=$161B^1$ ($161A^1$)	
			as $161B^1$, but plate smaller, narrower laterally=$161C^1$ ($161B^1$)	
			as $161B^1$, but plate simply convoluted longitudinally=$161C^2$ ($161B^1$)	
			as $161B^1$, but plate doubly convoluted longitudinally=$161C^4$ ($161B^1$)	

Table 15. (continued)

			opaque rod broad, flat, extended anterodorsally in chamber, no sclerite=$161C^3$ ($161B^1$)	
			opaque rod broad, flat, extended anterodorsally in chamber, no sclerite=$161B^2$ ($161A^1$)	
			opaque rod double-wide, but shorter than in 161^2, not expanded in chamber=$161C^5$ ($161B^2$)	
			very large, broad plate, extended around margins to fringes of dorsum=$161A^2$ (161^2)	
			opaque rod short, barely extended in chamber= $161A^3$ (161^2)	
162	Location of spermathecal duct insertion on spermathecal chamber	posterior/dorsal	anterior/dorsal=162^1	a,b,e
			anterior/middle=$162A^1$ (162^1)	
			anterior/ventral=162B ($162A^1$)	
			posterior/ventral=162^2	
			posterior/middle=$162A^2$ (162^2)	
			posterior/dorsal=$162A^3$ (162^2)	

Table 15. (continued)

			dorsal/posterior=$162A^4$ (162^2)	
163	Symmetry insertion of spermathecal duct	medial	slightly right of midline=163	a,b,e
			markedly right of midline=$163A^1$ (163)	
			slightly left of midline=$163A^2$ (163)	
164	Shape spermathecal duct	loosely, unevenly convoluted	sinusoidal, regularly wavy=164^1	a,b,e
			more or less straight=164^2	
			tightly, unevenly convoluted=164^3	
			loosely, unevenly convoluted=164A (163^3)	
165	Length spermathecal duct	medium	slightly short=165^1	a,b,e
			markedly short=$165A^1$ (165^1)	
			slightly long=165^2	
			markedly long=$165A^2$ (165^2)	
166	Diameter proximal portion of spermathecal duct	same as distal portion	dilated, markedly greater diameter than in distal portion=166	a,b,e

Table 15. (continued)

167	Diameter distal portion of spermathecal duct	narrow	slightly thick=167	a,b,e
			moderately thick=167A (167)	
			markedly thick=167B (167A)	
			extremely thick=167C (167B)	
168	Shape spermatheca	lanceolate, narrow, markedly arcuate	lanceolate, slightly arcuate, narrow=168^{1}	a,b,e
			lanceolate, thickened near apex, otherwise narrow=168A (168^{1})	
			vaguely lanceolate, somewhat convoluted, thickest subapically=168B (168A)	
			lanceolate, straight, narrow=168^{2}	
	Natural history:			
169	Center of life zone range	Canadian	between Canadian and Hudsonian=169^{1}	a,e
			Hudsonian=$169A^{1}$ (169^{1})	
			between Hudsonian and Arctic/Alpine=$169B^{1}$ ($169A^{1}$)	
			Arctic/Alpine=$169C^{1}$ ($169B^{1}$)	
			between Canadian and Transition=169^{2}	

Table 15. (continued)

			Transition=$169A^2$ (169^2)	
			between Transition and Upper Sonoran=$169B^2$ ($169A^2$)	
			Upper Sonoran=$169C^2$ ($169B^2$)	
170	Predominant microhabitat type	mesic forest floor	streamside=170^1	a,e
			lakeside=$170A^1$ (170^1)	
			perinival areas=$170A^2$ (170^1)	
			talus=$170A^3$ (170^1)	
			tundra=$170A^4$ (170	
			open seabeach=$170A^5$ (170^1)	
			tundra=170^2	
171	Life cycle timing	overwinter only or almost exclusively as larvae	overwinter as adults, in part only=171^1	a,b,e,
			overwinter only or almost exclusively as adults 171^2	
			overwinter as larvae, in part only=171A (171^2)	

Table 15. (continued)

[1] Each apotypic (derived) character state is given a unique code name in this table. For characters represented by only one apotypic state, the character number alone stands as code name for that apotypic state (e.g. character no. 2). Where two or more apotypic states have evolved from a single plesiotypic (primitive) state, the former are differentiated by different superscript numbers appended to the character number (e.g. character no. 4). For characters in which apotypic states have evolved sequentially from other apotypic (i.e. relatively plesiotypic) states, relatively apotypic states are coded by a combination of the character number and a capital letter (e.g. character no. 13). Note that capital letters used in the code here refer also to successive rows following the first row for a character listed in Fig. 372. Apotypic character states of characters with multiply-branched transformations have been coded with a combinations of character numbers, capital letters, and superscript numbers (e.g. character no. 1). Immediately following the code name for each subsequent apotypic state, code name of the derived state from which I judge it has evolved is noted in parentheses. My hypothesis on the transformation of each character can therefore be reconstructed directly from data presented in the table.

[2] Distributions of character states among members of Nearctic species and their Palaearctic relatives are presented in Fig. 372. In that figure, possession of an apotypic state is denoted by a solid square.

Table 15. (continued)

Open squares denote plesiotypic states. Notation here is just to facilitate cross-reference.

[3] Criteria used in evaluating the apotypy or plesiotypy of character states are discussed in the text. Code used here is as follows: a=ex-group comparisons; b=character correlations; c=group trends; d=correlation with adaptive significance; and e=in-group comparisons.

4.13 Phylogeny of Nearctic *Nebria*

Results of the cladistic analysis of Nearctic *Nebria* are presented in Fig. 373. This cladogram was chosen from among several through the procedure and according to criteria described above. It represents the simplest explanation (i.e. requires the fewest possible extra evolutionary steps--instances of parallelism, convergence or reversal) to account for the observed distribution of apotypic character states as presented in Table 15 and Fig. 372. I suggest that reference to these two data sources will permit rapid and accurate interpretation of the cladogram; and I will therefore confine discussion here to a few brief supplementary comments.

It has become customary to list, directly on a cladogram, the character states (or coded symbols for them) which demonstrate synapotypy for each lineage. I have found this impractical here, however, because of the large number of synapotypies involved. I have therefore chosen to list only the *number* of synapotypies found for each lineage (i.e. between any two nodes on the cladogram) without identifying the characters involved. Reference to Fig. 372 and Table 15 will permit recognition of synapotypies for any segment of the cladogram. Each hypothesis of relationship suggested by the cladogram is supported by at least five synapotypies (up to a maximum of 32). I therefore have considerable confidence in the accuracy of this reconstruction and look forward to the opportunity to test these hypotheses with data from new and independent character systems (e.g. external structure of larvae, pupae, and eggs; structure of various internal organ systems).

Monophyletic groups and inter-group relationships.--Based on the cladistic analysis of Nearctic species, I recognize four main groups of species. Synapotypic character states for each of these groups are listed under their respective descriptions (section 3.43).

As noted in the cladogram, the group comprising *N. virescens* and its Palaearctic relatives, the *virescens* lineage, is evidently the sister group of all other *Nebria* (including all Palaearctic species and groups not treated in this study [i.e. the so-called "endemic Palaearctic lineages" in Fig. 373]). This group is highly distinctive, its members easily distinguished from those of all other *Nebria* groups on the basis of numerous characters of male or female genitalia, mouthparts, pronotum, elytra, and legs. It would, perhaps, be appropriate here to recognize this group as a separate genus on the basis of 32 synapotypic features shared among members species. However, I prefer to make such a taxonomic decision only after a thorough review of inter-group relationships within Nebriini and between Nebriini and related tribes (e.g. Notiophilini, Opisthiini) has been completed.

Although the most parsimonious hypothesis of relationship (i.e. that requiring fewest extra evolutionary steps) between the *virescens* lineage and other nebriine groups is as suggested here, several discordant patterns of character state distribution are required by this arrangement of taxa. Most disturbing among these are patterns in several characters of male and female genitalia. For example, males of *N virescens*, *N. pusilla* Ueno, and *N. chalceola* Bates are unique among males of *Nebria* species considered here in shape of the basal bulb of the median lobe and of the dorsobasal piece and in the spatial

relationships between these two structures. Based on broad ex-group and in-group comparisons, I interpret each of the character states involved as apotypic. However, these states are also represented among males of Leistus and Notiophilus species (but not among those of Pelophila and opisthiine species). The same pattern is apparent among females for several characters of the coxostyli. There is, therefore, some evidence for closer phylogenetic relationship between the virescens lineage and Leistus and Notiophilus than between the former and all other Nebria species; but realignment of groups (i.e. rearrangement of taxa included in Fig. 369) based on this pattern of synapotypy creates discordance (and requires 20 extra evolutionary steps) in other characters. Also, six synapotypies (see Fig. 372) support the monophyly of a group including the virescens lineage and all other Nebria species and excluding Leistus and Notiophilus; and I therefore suggest that the preferred hypothesis comprises that set of relationships suggested by cladograms presented here (i.e. Figs. 369 and 373).

Sister group of the virescens lineage comprises all other species included in genus Nebria. Numerous subgenera have been proposed for groups of Palaearctic species; and, no doubt, some of these constitute monophyletic groups at some level of inclusiveness. I have studied representatives of each of these groups and conclude that they represent one or more independent lineages that diverged from the ancestral stock of the remaining Nearctic lineages and evolved independently in Eurasia. Relationships among these 'endemic Palaearctic lineages' are not yet clear, nor are they considered here further. Monophyly of the group comprising these lineages and the

Nearctic lineages (excluding the virescens lineage) is supported by five synapotypies, namely: (1) elytral microsculpture moderately impressed; (2) paraglossae completely fused (i.e. adnate) with ligula; (3) ventroapical margin of fourth hind tarsomere lobate laterally; (4) ventral surface of coxostylus asetose; and (5) opaque reinforcement rod in ventral wall of spermathecal chamber (bursa copulatrix) double-wide in midline.

The monophyly of the group including the remaining Nearctic species and their Palaearctic relatives in supported by 24 synapotypies (see Fig. 372). Three main groups included are the gyllenhali, gregaria, and metallica lineages. The gyllenhali lineage is judged to be the sister group of the other two together, a relationship supported by six synapotypies. This figure would be substantially greater if N. paradisi were excluded from the group. Members of this species exhibit a confounding mosaic of apotypic character states shared with both the remaining gyllenhali lineage species and those of the metallica and gregaria lineages. For example, all members of N. paradisi have frontal pale spots, an apotypic condition shared with all members of the metallica and gregaria lineages. In addition, N. paradisi females share with members of these lineages bursae copulatrices the longitudinal axes of which (in lateral aspect) are sigmoid, as opposed to the dorsally deflected condition exhibited by other females of the gyllenhali lineage. N paradisi females are the only ones among gyllenhali lineage species which have a dorsal sclerite on the spermathecal chamber, a condition shared with females of some but not all species of the other lineages. In contrast, apotypic states of characters of

male genitalia all support close phylogenetic relationship between *N. paradisi* and *N. sakagutii* and its relatives. Close phylogenetic relationship between the latter and the other species of the *gyllenhali* lineage is supported by numerous synapotypies. I choose to accept evidence from male rather than female genitalia in this instance. Apotypic states of bursal characters shared between *N. paradisi* females and those of the other lineages are, in fact, very slightly derived relative to the proposed plesiotypic states. It is therefore less difficult to accept their independent evolution than that of more unique and highly derived apotypic states shared by males of *N. paradisi* and other *gyllenhali* lineage species. Also, few *N. shibanaii* Ueno and *N. shiretokoana* Nakane adults have faint frontal pale spots. This suggests that tendency for development of frontal spots is not restricted to *N. paradisi* members among *gyllenhali* lineage species; and I therefore place little importance on this character as evidence against the relationship suggested here.

Seventeen synapotypies (see Fig. 372) support the monophyly of a group including the *gregaria* and *metallica* lineages. These two lineages are also highly distinctive as sister groups--11 synapotypies characterize *gregaria* lineage members and 17 distinguish those of the *metallica* lineage. Reconstruction of phylogenetic relationships of species within these lineages was relatively uncomplicated, except for specific instances. I found characters of female genitalia very useful in demonstrating relationships among *gregaria* lineage species. Unfortunately, I have not studied females of *N. angustula* Motschulsky, *N. charlottae* Lindroth, or *N. navajo* new species (females of the latter two species have not yet been collected); and placement

of these three species is therefore more tentative than that of other species in the lineage.

Relationships among members of the ovipennis species group (metallica lineage) were especially difficult to interpret. Males of all included species, except those of N. gebleri and N. mellyi Gebler,are characterized by a deep, basally-directed pouch on the right dorsolateral surface of the median lobe mid-shaft. Males of the two exceptional species have only a faint indentation of the mid-shaft surface at a corresponding point. Several apotypic character states are shared by N. mellyi, N. ovipennis, and N. spatulata members (e.g. loss of metallic reflection from elyta; reduced pigmentation (e.g. body color brown rather than black); elytral microsculpture very deeply impressed; elytral intervals faintly catenate). However, group trends are apparent in each of these characters, and these same apotypic states have evidently evolved repeatedly and independently in different groups. Close phylogenetic relationship among these three species is therefore unlikely (especially if distributional data are considered (see below)). Evidence suggests that, in fact, N. gebleri is the sister group of all the other ovipennis group species. Seventeen synapotypies characterize the group exclusive of N. gebleri (whereas, if N. mellyi is excluded and N. gebleri included, only two synapotypies distinguish the resulting group). The difference between these alternative sets of relationship is, however, not as great as is apparent . Several synapotypies for the group exclusive of N. gebleri involve characters transformations of which are involved in group trends associated with wing reduction (e.g. changes in shape of elytra, length of legs, length of metasterna, etc.). In spite of the

reduced significance of differences in number of synapotypies and the more complex hypothesis required to account for the geographical distributions of group members (see discussion in section 4.2), I suggest that intra-group relationships are best interpreted as presented in the cladogram.

In general, relationships suggested from the cladistic analysis were similar to those I expected intuitively, based on observations over the course of my study. Differences were, in each instance, due to my recognition of similarities which now appear (from the analysis) to represent symplesiotypies. Two sets of relationships, however, were particularly unexpected; and I am not yet satisfied that these reflect evolutionary histories of the species involved. The first of these is the group which comprises _N. arkansana_, _N. fragilis_, and _N. zioni_. I anticipated that closest phylogenetic relationship would be demonstrated between _N. arkansana_ and _N. fragilis_. Cladistic analysis suggests that _N. fragilis_ and _N. zioni_ are more closely related to each other than either is to _N. arkansana_. Similarly, I expected to confirm closer relationship between _N. eschscholtzii_, _N. desolata_, and _N. navajo_ new species than between _N. diversa_ and any one or more of these. However, analysis suggests that _N. diversa_ and _N. eschscholtzii_ are sister species and together serve as the sister group of _N. desolata_ and _N. navajo_. My reasons for doubting these sets of relationships were mainly based on distributional patterns and tentative scenarios formulated (intuitively) for the distributional histories of these taxa. Although alternative scenarios consistent with those sets of phylogenetic relationships suggested from cladistic analysis actually require less complex explanations for observed

distribution patterns than those I constructed originally, I am not yet convinced that cladistic analysis of structural characters, alone, is capable of recognizing a particular set of conditions and sequence of evolutionary events which may have pertained in these instances.

A hypothetical example may demonstrate this point. Consider a species, A, in which geographical variation in one or more characters is clinal (Fig. 371A), ranging from a plesiotypic character state at one geographical extreme to an apotypic state at the other. At some point in time, the range of this species is split by some barrier (as in Fig. 371B) so that members of populations on both sides of the barrier exhibit the apotypic state(s). Speciation follows, producing species A_1 and A_2 (Fig. 371C). The range of species A_1 is subsequently split (in Fig. 371D), resulting in isolates which do not share the derived state(s). If and when speciation occurs (Fig. 371E) producing species B_1 and B_2, a curious situation arises. Species B_1 and B_2, which are in fact closest phylogenetic relatives (i.e.sister species), do not share the apotypic state(s) of this(these) character(s), but species A_2 and B_2 do so. Cladistic analysis would therefore suggest closest relationship between A_2 and B_2 in the absence of contradictory data--a misinterpretation of the evolutionary history.

If populations of _N. eschscholtzii_, _N. desolata_, and _N. navajo_ were considered presently conspecific, cumulative patterns of geographical variation in several characters (e.g. body and appendage color, shape and depth of impression of elytral and pronotal microsculpture) would be apparent which closely approximate the pattern presented in the above example (Fig. 371A). Similarly, if

populations of _N. arkansana_, _N. fragilis_, and _N. zioni_ were considered presently conspecific, cumulative variation patterns, although less obvious, would also approximate that of the example. The sequence of events suggested in the example _could_ therefore have followed, given operation of some factors (such as changes in climate) which could promote successive divisions of the cumulative ranges of each of these groups, resulting in the present geographical distributions and diversity of species. I can at present suggest no tests of these hypotheses other than a search for synapotypies among species presumed to be most closely related. Results of the cladistic analysis have already shown, however, that on this basis, other hypotheses of relationship are preferred. Perhaps data from additional character systems will eventually support one of these alternative hypotheses.

Twenty Palaearctic species are judged to be closely related to Nearctic species; and these are distributed among eight different groups. Zoogeographic implications of proposed relationships are discussed in section 4.3 below.

Hypothetical common ancestor of Nearctic Nebria.--Together, character states listed in Table 14 and the plesiotypic states listed in Table 15 describe a hypothetical common ancestor for Nearctic _Nebria_ species, based on both the evolutionary classification of characters and the cladistic analysis of taxa. There is no reason to believe nor need to suggest that any organism (or group of same) so characterized ever existed. Such hypothetical ancestors function only for defining evolutionary baselines, thereby providing perspective on evolutionary change within and between groups. They are especially useful as aids in recognizing sister groups, a task otherwise made difficult by the

great divergence between living representatives of even close phylogenetic relatives.

Convergence and reversal.--An important assumption made in cladistic analysis and in subsequent reconstruction of phylogenetic relationships is that, in the evolution of organisms and of characters, divergence is more common than convergence (including parallelism) or reversal. Synapotypy is therefore more likely to arise as a result of common ancestry than from convergence or reversal; and it can then be used to recognize groups descendant from a common ancestor. I therefore agree with Ball (1975) that "it is important to note similarities apparently not the result of descent from a common ancestor", not only because "such similarities give clues to the major selective forces at work on members of the genus and might give clues to other interpretations of relationship", but also because they serve as tests of the basic assumption. Once characters have been analysed, their transformation series have been established, and a set of hypotheses on phylogenetic relationships of taxa have been selected (based on criteria outlined above), characters themselves may then be re-examined in light of these relationships for instances of convergence or reversal.

Using the set of phylogenetic relationships presented in the cladogram (Fig. 373) and the classification of characters presented in Table 15, I re-analyzed data on distributions of character states and transformations of characters to identify and quantify instances and sources of similarity not due to common ancestry. I use the term extra evolutionary step for any instance of convergence (independent acquisition of a relatively apotypic character state) or reversal

(acquisition of a relatively plesiotypic character state). I make no distinction here between parallelism and convergence. Extra evolutionary steps arise from two sources. First, they may be intrinsic to the transformation series of a character. For example, in the transformation of character no. 96 (Table 15), relative leg length, states 96^1 and $96C^2$ are convergent--i.e. have apparently evolved from two different relatively plesiotypic states, namely the plesiotypic state and state 96B, respectively. Reversals may also be intrinsic to transformations (e.g. character no. 83, continuity of elytral intervals, in which two reversal steps are apparent). Intrinsic extra evolutionary steps can be likened to alternative pathways to the same (evolutionary) destination (i.e. similarity).

The second source of extra evolutionary steps is simply independent acquisition of a particular character state (i.e. extending the analogy used above, use of the same pathway two or more times); and most extra evolutionary steps arise in this manner. I term these extrinsic extra steps because they do not require changes in the number or sequence of states in transformation series.

The 171 characters analysed comprise a total of 670 apotypic character states. If hypotheses on character transformations and phylogenetic relationships among species are correct, a total of 1468 extra evolutionary steps are required to account for the distribution of character states among Nearctic *Nebria*. This figure represents the sum of all intrinsic and extrinsic extra steps for all characters and character states, including a number of logical extra steps, which include those instances in which convergence is implied by reference to transformation sequence although not evident as similarity. For

example, in members of N. pusilla (species no. 3, Fig. 372), elytral humeri (character no. 77, state 77E, Table 15) are completely obliterated. Although this character state is autapotypic for members of this species, evolution must have followed a sequence similar to that proposed for the transformation of the character (Table 15). Because members of N. chalceola, the sister species of N. pusilla, exhibit rectangular humeri (the primitive condition), it is logical to record an instance of convergence here with similar transformations in other lineages.

I find the number of extra evolutionary steps noted above to be unexpectedly high, although no baseline for comparison has been provided by previous studies on convergence or reversal in carabid beetles. Data presented by Ball (1975), Erwin (1970), and others were not generated from equally comprehensive analyses of either characters or character states. My findings are, therefore, incommensurable. I must also mention that alternative sets of hypotheses on phylogenetic relationship and on transformations of characters were evaluated; but in each instance, many additional steps were required to account for character state distributions.

In order to facilitate interpretation of and future comparisons with my findings, I examined sources of these extra evolutionary steps in greater detail. For example, by calculating the frequency distributions of characters in which a given total number of intrinsic and extrinsic extra evolutionary steps are required, results represented in Fig. 374 were obtained. The mean number of extra steps required per character is 8.7018; and only 28 (16% of) characters analysed exhibit character state distributions which do not require

extra steps. The mean number of intrinsic extra steps alone per character, however, is only 0.538; and 114 (66.7% of) characters have no extra steps in their transformations (Fig. 375). A comparison of intrinsic extra steps due to convergences (Fig. 376) with those due to reversals (Fig. 377) indicates that reversal steps are more common (mean equal to 0.380 reversal steps per character) in transformation series than convergent steps (mean equal to 0.164 convergent steps per character). Also, the percentage of characters with one or more (range one to three) reversals in their transformation series is greater than that for characters with one or more intrinsic convergent steps (range one to two) (29.9% and 13.45%, respectively).

Because characters differ significantly in number of apotypic states in their respective transformation series (range from one to 14 states), a more appropriate level of comparison may be the character state. I therefore calculated frequency distributions for character states independently. Without a context of respective transformation series, however, I could not relate intrinsic extra steps to particular states in every instance. I therefore analysed character state frequency distributions only for extrinsic extra steps and compared those due to convergence with those due to reversal. Apparently, 337 character states (50.3%) have been acquired more than once (range in single character states from one to 20 instances) (Fig. 378), and the mean number of times each state has been acquired is 1.960. [Extra steps considered convergences do not include repeated acquisition of states considered reversals (the latter are counted as reversal steps)]. In contrast, only 64 character states (9.6%)

represent reversal steps which have been acquired one or more times (range in single states from one to 8 instances) (Fig. 379); and, on average, only about one state in five represents a single reversal step (i.e. mean number of reversals per character state equals 0.215). This relationship is in marked contrast to that noted above for intrinsic steps. It appears that, although reversal steps are more common than convergence steps in transformation series, the frequency with which Nebria members have evolved along reversed pathways is much lower than that along convergent pathways. The extent to which this generalization may reflect the effects of genetic factors and selective forces limiting reversals and/or divergence (thereby promoting convergence) is unknown.

Range in total number of intrinsic and extrinsic extra evolutionary steps per character is quite large (from zero to 36 steps); and the frequency distribution of extra steps per character is presented in Fig. 374. Most, but not all, characters for which numerous extra steps are required are the same as those in which group trends have been recognized (see section 4.11). Characters correlated with hindwing size and color and microsculpture characters comprise a majority of these. Strong selective forces appear to favor these evolutionary trends. However, a few characters in which many extra steps are required do not belong in this category. Shape of antennal scape (character no. 39, Table 15 and Fig. 372) is represented by only four apotypic character states; yet at least 36 instances of convergence have occurred among them (e.g. state no. 39^1, scape slightly narrowed basally, has been independently acquired at least 21

times). Again, strong selective forces must be at work on the expression of this character; but the pattern of distribution of its states among _Nebria_ species is almost random. Oddly, this character is often extremely useful in distinguishing members of closely related species, of different subspecies, or of other allopatric populations of a species. Intraspecific and/or intrapopulational variation is, in most instances, very low or essentally absent. It is difficult to reconcile this paradoxical pattern (i.e. high degree of convergence and plasticity evident interspecifically and very low variation within species, subspecies, or populations); but I suggest that this character may be important for species recognition among members, an hypothesis I hope to test with observations later.

The above example is a good one to illustrate a final point; namely, that characters which exhibit frequent convergence or reversal in their evolution may still be useful as descriptors if intra-taxon variation is low. Such characters may also be useful in cladistic analysis, if only as an aid in recognizing relationships between two or a few species. Each character may have some limited use and should not, therefore, be rejected _a priori_ on the basis of its complexity alone.

The large number of extra evolutionary steps noted here may cast some doubt on the correctness of the basic assumption made above on the origins of similarity. I have at present no way to evaluate this test of the assumption. However, if we assume for a moment that associations of character states exhibited by members of different species are acquired at random rather than by descent, the number of possible unique distributions of 670 character states representing

171 characters among 62 species is too large to comprehend. In comparison, the 1468 extra evolutionary steps required by sets of hypotheses proposed here on the evolution of characters and the phylogenetic relationships of species are insignificant and, I suggest, indicative of a very high degree of non-randomness. I therefore continue to accept the assumption as a working hypothesis until a better general hypothesis is proposed.